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THE UNIVERSITY OF ALBERTA

A REVISION OF THE ENCALYPTACEAE (MUSCI) WITH PARTICULAR REFERENCE TO THE NORTH AMERICAN TAXA

by

Ⓒ DIANA G. HORTON

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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Encalypta ciliata Hedwig

THE UNIVERSITY OF ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "A Revision of the Encalyptaceae (Musci) With Particular Reference to the North American Taxa" submitted by Diana G. Horton in partial fulfilment of the requirements for the Degree of Doctor of Philosophy in Bryology.

Dale H. Vitt
Supervisor

Walter Moser

External Examiner

Date December 31st, 1980

To my parents, Betty and Harry Horton,
who laid the foundation for this work many years ago
when they instilled in me their appreciation of the natural environment.

ABSTRACT

The Encalyptaceae, with two genera, Bryobrittonia and Encalypta, are defined by a mitrate, long-cylindric calyptra. Bryobrittonia is monotypic, and plants are characterized by upper laminal cells with protruding, but smooth walls. Nineteen species and one subspecies of Encalypta are recognized, with plants characterized by upper laminal cells having protruding, papillose walls. Important taxonomic features include the shape and color of the calyptra, the type of peristome (or the lack of one), the shape and color of the capsule, the color and length of the seta, the overall coloration of the vegetative portion of the plants, color and prominence of the costa on the abaxial surface of the leaf, structure of the abaxial surface of the costa, shape of the leaves, position of margins, color and definition of the basal cells, and presence or absence of a basal, marginal border. Species of Encalyptaceae are concentrated in northerly, montane regions of the Northern Hemisphere, but three of the species of Encalypta also occur in the Southern Hemisphere, and two others are endemic to South America. The plants grow in rock outcrop and tundra habitats. On the basis of quantitative data, it is apparent that substrate-type is an important factor governing the occurrence of species of Encalyptaceae. Bryobrittonia longipes, E. longicolla, E. mutica E. procera and E. spathulata occur almost exclusively on substrates with a pH above 7.0, while E. brevicolla and E. brevipes are restricted to substrates with a pH below 6.5. Encalypta affinis, E. alpina, E. ciliata and E. rhaptocarpa occur on both siliceous and calcareous substrates, but show a marked preference for one type or the other.

Inter-relationships among the species of Encalyptaceae are primarily determined on the basis of the shape and color of the calyptra, the peristome-type, the length of the seta and leaves, and the spore-type. The species with a long, dark calyptra, the rostrum little differentiated from the cylinder and the base of the cylinder lacerate, a double peristome with the two layers more-or-less unfused, a long seta and long leaves, and small, green spores that are isopolar are considered to most closely approach the ancestral type among the extant species of Encalyptaceae. These are B. longipes, E. streptocarpa and E. procera. The most highly derived species, including E. armata, E. asperifolia, E. brevipes, E. flowersiana, E. intermedia, E. microstoma, E. mutica and E.

spathulata, are characterized by a short, pale calyptra, the rostrum distinctly differentiated from the cylinder and the base of the cylinder fringed, no peristome, a short seta and short leaves, and larger, brown spores that are more-or-less distinctly heteropolar. Four groups of species of *Encalypta* are recognized and all of these are considered to be ultimately derived from *E. streptocarpa* or a closely related, but now extinct, ancestor. The *E. procera*–*E. streptocarpa* group is defined as outlined above, the *E. rhaptocarpa*–*E. vulgaris* complex is differentiated by distinctly heteropolar spores with large, verrucose protuberances on the distal surface, the *E. affinis*–*E. ciliata* lineage is difficult to characterize as a whole, but individual species are linked by common apomorphous character-states, the *E. alpina*–*E. longicolla* group contains species of uncertain affinities, but believed to be most closely related to one another. Species of Encalyptaceae are considered most closely related to the Pottioideae (Pottiaceae) on the basis of similarities in leaf shape and laminal cell structure, shape of the capsule, structure of the peristome and annulus, and chromosome number.

It is speculated that species of Encalyptaceae evolved in Laurasia prior to the separation of the North American and Eurasian continents. The widespread, but relictual, distribution pattern of some species with many apomorphous character-states, for example, *E. brevipes*, indicates that such species probably evolved prior to, or around the time of, separation of the northern continents. However, several other species, including *E. armata*, *E. asperifolia*, *E. flowersiana* and *E. microstoma*, that are also characterized by a number of apomorphous character-states have a very restricted pattern of distribution. Such species are considered to have evolved relatively recently in Tertiary times.

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I. INTRODUCTION

The Encalyptaceae are a small family of predominantly Northern Hemisphere mosses with only two genera, one of which is monotypic. However, they are an important component of northerly montane and arctic vegetation. The family is clearly defined by the distinctive, long-campanulate calyptra and this feature is emphasized in the common names of 'extinguisher moss' and 'Glockenhut' that date back to the earliest descriptions of species of Encalypta. The Encalyptaceae have long been a source of interest and phylogenetic speculation because of the diversity of peristome-types that occur in the family. Species of Encalyptaceae predominate in such phytogeographically important regions as the Western Cordillera in North America, and Fennoscandia and the Alps in Europe, yet the ranges of the species have been incompletely documented, particularly in North America and Asia, and a number of taxa have been a source of taxonomic confusion. The present study is an attempt to define the taxa in the Encalyptaceae, primarily on the basis of structure, in order to clarify the family taxonomically on a world-wide basis; to delineate the habitat and range of each taxon, particularly in North America; and to suggest what might be the phylogenetic relationships among the taxa, as well as how the family is inter-related with other groups in the Musci, based upon an analysis of trends in character-state evolution within the Encalyptaceae, and the habitat preferences and distribution patterns of individual taxa.

Historical Perspective

One of the earliest descriptions of a species of Encalypta is that of "Muscus trichoides minor pileis magnis acutis. The Extinguisher Moss." published by Petiver in 1695 (Horton 1979a). Further descriptions of species of Encalypta are in Dillenius (1741) (in the genera Bryum and Hypnum), Hedwig (1787, 1789 and 1801), Bridel (1798, 1806) and Schwaegrichen (1811), but Hedwig, Bridel and Schwaegrichen also included species that are presently considered to belong to other genera in their concepts of Encalypta (or Leersia) (Horton 1979a). It was not until 1819 that Bridel limited the genus Encalypta to include only those species with the distinctive calyptra. The genus was delimited on this basis until 1953 when Steere reported the monotypic Bryobrittonia to be characterized by the same calyptra-type. This stability in the generic concept of Encalypta is particularly noteworthy because a number of authors have recognized subdivisions within the genus. In some instances the divisions reflect a stress upon the different peristome-types that occur in the genus, while others are based upon other sporophytic features. Gametophytic structure has also been considered to be important in one infrageneric treatment.

Nees, Hornschuch and Sturm (1827) were the first to point out that the structure of the peristome is not the same in all species of Encalypta. They remarked that "Das Peristom zeigt für diese kleine Gattung, die im Ganzen so übereinstimmende Arten enthält, höchst merkwürdige Anomalie.", and divided the genus into two sections aperistomae and peristomae (Table 1). However, it is clear from their discussions and arrangement of the individual species in the text that these were purely artificial groupings, and Nees, Hornschuch and Sturm (1827) did not consider these to represent natural relationships. Bruch, Schimper and Gümbel (1838) similarly emphasized the extraordinary variation in the peristome among a group of species otherwise so naturally cohesive. They divided species of Encalypta into three groups based on peristome absent, simple or double (Table 1). Later Schimper (1876) recognized four sections in Encalypta also based on differences in the peristome. But he also divided Bruch, Schimper and Gümbel's (1838) group of species with simple peristomes into two types; those with a simple, more-or-less well-developed or absent peristome, and those with a simple, regularly developed peristome (Table 1). Philibert (1889) reported that the genus Encalypta can be divided into three principal sections because the peristomes that occur in the genus represent three different types; however, he did not designate names for the three sections (Table 1). Limpricht's (1890) treatment of the Encalyptaceae in Rabenhorst, which was published shortly after Philibert's (1884-1890) studies of the different peristome-types in the Musci (see below), was the first to incorporate some of Philibert's ideas into infrageneric divisions of Encalypta (Table 1). Coker (1918) recognized two sections within Encalypta, the Haplolepideae and Diplolepideae (Table 1), and Flowers (1938) incorporated these same concepts.

Table 1. SUBDIVISIONS OF THE GENUS ENCALYPTA.*

Nees, Hornschuch & Sturm (1827)	Bruch, Schimper & Gumbel (1838)	Schimper (1876)	Carl Müller (1848-1849)	Lindberg (1879)
I. Aperistomae	**a. Peristomio nullo**	**Sect. I.** Peristomium nullum.	**Sectio I. Psilotheca**	**A. Rhabdotheca**
E. vulgaris E. commutata [= E. alpina]	E. commutata [= E. alpina]	E. commutata [= E. alpina]	a. Peristomium nullum E. commutata [= E. alpina] E. microstoma	L. contorta [= E. streptocarpa] L. procera [= E. procera] L. rhaptocarpa [= E. rhaptocarpa L. extinctoria [= E. vulgaris L. spathulata [= E. spathulata] L. alpina [= E. alpina]
II. Peristomae E. ciliata E. apophysata [= E. affinis] E. rhaptocarpa E. streptocarpa	**b. Peristomio simplici** fugacissimo E. vulgaris	**Sect. II.** Peristomium in eadum specie simplex 16-dentatum, plus minus perfectum vel nullum. E. vulgaris E. rhaptocarpa E. ciliata	b. Peristomium simplex E. vulgaris E. ciliata E. apophysata [= E. affinis] E. longicolla E. brevicolla	
	peristomio persistente E. ciliata E. apophysata [= E. affinis] E. longicolla E. longicolla var brevicolla [= E. brevicolla] E. rhaptocarpa	**Sect. III.** Peristomium simplex regulariter evolutum. E. apophysata [= E. affinis] E. longicolla E. brevicolla	**Sectio II Rhabdotheca** E. spathulata E. rhaptocarpa E. streptocarpa E. procera	**B. Psilotheca** L. brevicolla [= E. brevicolla] L. affinis [= E. affinis] L. laciniata [= E. ciliata]
	C. Peristomio duplici florescentia monoica E. procera florescentia dioica E. streptocarpa	**Sect. IV.** Capsula striata, sicca spiraliter torta; peristomium duplex E. procera E. streptocarpa		

Table 1. Continued.

Philibert (1889)	Limpricht (1890)	Kindberg (1897)	Brotherus (1902)	Coker (1918)
i. E. longicolla E. brevicolla E. apophysata [= E. affinis]	A. Peristom fehlend E. commutata [= E. alpina] E. vulgaris E. spathulata	**I. Streptotheca** E. contorta [= E. streptocarpa] E. procera	**Sect. I. Pyromitrium** E. alpina	**Haplolepideae** E. alpina E. extinctoria [= E. vulgaris] E. laciniata [= E. ciliata] E. rhaptocarpa
ii E. procera E. streptocarpa	B. Peristom einfach und nach dem Typus, der Aplolepideen gebaut E. ciliata E. ciliata var. microstoma [= E. microstoma] E. rhaptocarpa	**II. Diplolepis** E. longicolla E. affinis E. brevicolla	**Sect. II. Xanthopus** E. ciliata E. ciliata var. microstoma [= E. microstoma]	**Diplolepideae** E. apophysata [= E. affinis] E. brevicolla E. procera E. contorta [= E. streptocarpa]
iii. E. ciliata E. rhaptocarpa E. vulgaris E. commutata [= E. alpina]	C. Peristom dopelt, nach dem Typus der Diplolepideae gebault, das innere dem äussern anhängend, oft nur in Hautfetzen angedeutet, selten mit Cilien E. apophysata [= E. affinis] E. longicolla E. brevicolla E. contorta [= E. streptocarpa] E. procera	**III. Rhabdotheca** E. vulgaris E. rhaptocarpa E. spathulata	**Sect. III Rhabdotheca** E. vulgaris E. mutica E. spathulata E. intermedia E. asperifolia E. rhaptocarpa	
		IV Pyromitrium E. alpina	**Sect. IV. Diplolepis** E. longicolla E. affinis E. brevicolla	
		V. Xanthopus E. ciliata E. ciliata subsp. microstoma [= E. microstoma]	**Sect. V. Streptotheca** E. contorta [= E. streptocarpa] E. procera	

Table 1. Continued.

*In order to facilitate comparison between different treatments, I have omitted some species that would be redundant according to present taxonomic concepts (for example, Nees, Hornschuch and Sturm (1827) included both *E. apophysata* and *E. cylindrica*, which are synonyms of *E. affinis*, in their group peristomae; therefore I have omitted *E. cylindrica*); I have modified the lists in Müller (1848–1849) and Kindberg (1897) so as not to confuse what their concept of a particular group was (for example, Kindberg (1897) included *E. macounii*, which is actually synonymous with *E. affinis*, in Pyromitrium; however, Kindberg's concept of *E. macounii* was such that it should in this instance be considered a synonym of *E. ciliata*; and I have followed author's citations of infrageneric taxa only when that taxon is currently recognized as a species (for example, Brotherus (1901–1902) considered *E. microstoma* as *E. ciliata* var. *microstoma*, but I have not included Lindberg's citation of *L. rhaptocarpa* var. *leptodon* because this is presently considered to be synonymous with *E. rhaptocarpa*).

Carl Müller's (1848-1849) subdivision of Encalypta into two sections, Psilotheca and Rhabdotheca, is based upon differences in the shape of the capsule. Species placed in the section Psilotheca were considered to have the theca smooth and estriate, which included species both with and without a peristome (Table 1). The section Rhabdotheca is defined by a plicate theca. Among the species included in this section, some have a double peristome, one a single and one lacks a peristome (Table 1). Lindberg (1879) cited these same sections in the genus Leersia, but reversed their order and placed E. alpina in the section Rhabdotheca rather than in Psilotheca where Müller has it (Table 1).

The most extensive subdivision of Encalypta is that of Kindberg (1897), who recognized five infrageneric categories (the precise rank is not indicated) (Table 1). Kindberg's (1897) basis for these subdivisions is somewhat complicated because it includes a combination of gametophytic and sporophytic features. The essential features of the five groups are outlined in Table 2. Brotherus (1902, 1924) followed Kindberg's (1897) treatment, except that Brotherus reversed the order of the sections and began with Pyromitrium (Table 1).

Various opinions as to the systematic position of Encalypta are reflected in the placement of this genus relative to other moss genera in treatments of the Musci. Limpricht (1890) observed that "Diese Gattung, eine der Schönsten moosgattungen, hat, weil sie in ihren verwandtschaftlichen Beziehungen nach verschiedenen Richtungen ausstrahlt, eine feste Stellung im Systeme noch nicht gefunden.". Bruch, Schimper and Gümbel (1838) and Schimper (1855) placed the Encalyptaceae after the Tetraphideae and before the Zydodontaceae and Orthotrichaceae, while Müller (1848-1849) stationed Encalypta in the Calymperaceae, with Calymperes and Syrrhopodon, next to the Pottiaceae. De Notaris (1869) put the monotypic Encalyptacei after the Orthotrichacei and before the Polytrichacei, and Schimper (1876) reversed the order he had earlier published in the Corollarium situating the monotypic subfamily Encalypteae after the Orthotricheae in the family Grimmiaceae and before the Tetraphidaceae. Lindberg (1879) placed Encalypta (as Leersia) in the subfamily Leersieae next to the Tortuleae in the Tortulaceae. Philibert (1884) stated that "Les Encalyptées pourraient donc être considérées comme le point central d'ou les autres formes de mousses auraient divergé.", and suggested that the Encalyptaceae are most closely related to Orthotrichum in one

Table 2. THE ESSENTIAL FEATURES OF KINDBERG'S (1897) SUBDIVISIONS OF ENCALYPTA

	Peristome	Capsule	Calyptra	Leaves
I. Strepthotheca	double; exostome and endostome well-developed.	twisted; rarely with neck.	very long; fringed.	bordered.
II. Diplolepis	double; endostome rudimentary and adherent to exostome.	smooth; neck present.	usually fringed.	not bordered.
III. Rhabdotheca	single, often present.	plicate.	not long; rarely fringed.	often bordered.
IV. Pyromitrium	absent.	smooth.	long; fringed when young.	bordered.
V. Xanthopus	absent.	smooth.		indistinctly bordered.

sense, to Barbulacées [=Pottioideae] in another, and in a third to Polytrichaceae, Tetraphidaceae, and *Buxbaumia* and *Diphyscium*. Limpricht (1890) considered the Encalyptaceae, which was placed between the Orthotrichaceae and the Georgiaceae [=Tetraphidaceae], to contain two genera, *Encalypta* and *Merceya*. Kindberg (1897) followed this except that he placed the Encalyptaceae between Calymperaceae and Orthotrichaceae. Müller (1901) reported the Encalyptaceae to consist of three genera, *Encalypta*, *Streptocalypta* and *Merceya*, with the family following the Calymperaceae and preceding the Pottiaceae. Fleischer (1904) divided the arthrodontous Bryales into three groups, the Haplolepideae, Heterolepideae and Diplolepideae. The Heterolepideae, with the single family Encalyptaceae, is placed between the Grimmiaceae at the end of the Haplolepideae and before the Funariaceae in the Diplolepideae. In the first edition of Engler and Prantl, Brotherus (1902) considered the Encalypteae to be monotypic and positioned it after the Pottieae in the Pottiaceae, before the Grimmiaceae and Orthotrichaceae. In the second edition (Brotherus 1924), he similarly considered the Encalyptaceae to be monotypic, but placed it after the Calymperaceae and before the Pottiaceae. Coker's (1918) treatment is the only previous revision of the Encalyptaceae and she treated the Encalyptaceae as a monotypic family closely related to the Pottiaceae. Grout (1937-1938) placed the Encalyptaceae, which Flowers (1938) considered to be monotypic, after the Calymperaceae and before the Buxbaumiaceae. In 1953, Steere reported that the formerly unknown sporophytes of *Bryobrittonia* are almost indistinguishable from those of *E. streptocarpa* and *E. procera*, and that the calyptra of *Bryobrittonia* is typically encalyptaceous. Therefore, he included *Bryobrittonia*, which had formerly been considered to belong in the Pottiaceae (*cf.* Brotherus 1924 and Grout 1939), as a second genus in the Encalyptaceae. Later, Savicz-Ljubitskaja and Smirnova (1970) recognized *Encalypta* and *Bryobrittonia* in the Encalyptaceae, which they placed in a separate order the Encalyptales after Fissidentales and prior to Pottiales and the Pottiaceae. Recently, Stone (1977) suggested that the Bryobartramiaceae may be closely related to the Encalyptaceae. In conclusion, there has been no consensus of agreement historically, but the genus *Encalypta* has generally been placed close to either the Pottiaceae-Calymperaceae or the Orthotrichaceae. Few of the authors cited above give reasons for their placement of families in a particular arrangement; however, there are vegetative similarities in the leaves of Encalypta with both the Pottiaceae and the Orthotrichaceae, and the calyptra of Encalypta with the Orthotrichaceae and some genera of Pottiaceae. It is apparent that the fundamental difference between these positions is that peristomes in the Pottiaceae are of the haplolepideous type and that those in the Orthotrichaceae are of the diplolepideous type.

Having cited above many of the major treatments that deal with the genus Encalypta, it is perhaps appropriate to mention a few of these that I have found to be particularly excellent and/or are of importance in an historical context. Among the very early works, Hedwig's (1787) Descriptio et Adumbratio Microscopico-Analytica Muscorum Frondosorum, published in both Latin and German language editions, contains lengthy descriptions of two species of Encalypta, but it is the incredibly detailed, hand-colored plates that make this work an unequaled contribution. Bridel's circumscription of the genus Encalypta is of fundamental importance and actually dates back to 1798 in the Muscologia Recentiorum where his infrageneric division separates species currently considered to belong to genera other than Encalypta from those presently accepted as species of Encalypta. Among the leading bryologists of the time, including Hedwig and Schwaegrichen, Bridel was apparently the only one who grasped that species of Encalypta, when defined by the campanulate calyptra, formed a natural group distinct from other taxa with which they were generally grouped.

I have been ever more impressed by the depth of Nees, Hornschuch and Sturm's (1827) Bryologia Germanica. It is truly remarkable for its time. Their introductory discussion of the essential features that define species of Encalypta can hardly be improved upon, and their characterization of species of Encalypta as "...Moose der kalten Zone, und der Gebirge und Alpen der nordlichen Erdhälfte;..." remains accurate today. However, it is interesting to see the state of knowledge at that time reflected in their statements that they knew of no Encalypta species in the Southern Hemisphere and that of the eight species they recognized, all of which were native to Germany, only a single one was then known from North America (E. vulgaris from "Ounalaska"). Nees, Hornschuch and Sturm (1827) were the first authors to piece together the early history of the genus Encalypta. They were also the first to subdivide the genus on the basis of differences in the peristome, as noted above. Their lengthy treatments of the individual species included a brief characterization of the essential features of that species in Latin and German, the German common name, an exhaustive list of synonyms and citations of earlier treatments, a detailed description, discussion of habitat, date of maturity of the sporophyte, and a figure, as well as taxonomic remarks. In many respects, Bryologia Germanica is at least equal to Bryologia Europaea and in some aspects surpasses the treatment of Encalypta in the latter work. However, there are two or three rather obvious limitations to Bryologia Germanica. There is an overemphasis on minute details of structure of the male and female "flowers", and the species concepts are very narrow in one or two instances (for example, E. apophysata [=E. affinis subsp. affinis] and E. cylindrica [=E. affinis subsp. affinis] are treated as distinct species and reported to be very easily differentiated). Also, the geographical area covered is more restricted than in Bryologia Europaea. These may be the major reasons that Bryologia Germanica has not received greater recognition.

Bruch, Schimper and Gümbel's (1838) Bryologia Europaea is another outstanding contribution. While Nees, Hornschuch and Sturm (1827) had treated six of the species of Encalypta that are presently recognized, nine are included in Bryologia Europaea. The introductory portion of the treatment in Bruch, Schimper and Gümbel (1838) includes a wealth of information on the developmental morphology of plants of Encalypta, as well as dealing with structure of the plants and history of the genus. The illustrations, although pleasing to the eye and finely detailed, are, in some respects, disappointingly inaccurate. For example, quite obvious specific differences in the shape of the calyptra are not faithfully represented.

Philibert's (1884, 1889) detailed descriptions of the structure of the peristome of a number of species of Encalypta are still the most complete reference for this subject, and there is evidence to support his suggestion that this family is of central significance in the evolution of mosses. (A more extensive discussion of Philibert's contribution follows.)

Limpricht's (1890) contribution to Rabenhorst's Kryptogamen-Flora includes eleven species currently accepted, although the treatments of two of these, E. brevicolla and E. procera, are abbreviated. His descriptions are not only detailed, but modern and extremely accurate, and the notes on habitat indicate a good understanding of the species in the field. I have found this to be a reliable source for clarification of historical details not included in Bryologia Germanica or Bryologia Europaea. Although Limpricht's treatment was completed almost a century ago, it still ranks among the best modern analyses of species of Encalypta.

In 1918, Coker revised Encalypta in North America. Her revision is of particular interest because the taxonomic status of a number of species reported to be endemic to North America, including those described by Austin, Kindberg and Mitten, was assessed. In the introduction to this treatment, Coker stated that 18 species of Encalypta had been reported to occur in North America north of Mexico and that this number had been reduced to eight. In a footnote she added "The responsibility for these reductions rests largely with Mrs. Britton.". I suspect, on the basis of this comment and an earlier publication (Britton 1895), which indicated Britton had spent some time studying specimens of Encalypta, that the fundamental taxonomic and nomenclatural decisions in Coker's revision should probably be attributed primarily to Elizabeth Gertrude Britton. However, the descriptions and illustrations are Coker's; her notes are still preserved with the specimens in the New York Botanical Garden.

Flowers (1938) recognized the same North American species of Encalypta that Coker had (1918), although his concepts of some of the infraspecific taxa are different. The depth of Flowers' understanding of the taxa is apparent in his discussions of diagnostic features, habitat and variation. Flowers' treatment, as Limpricht's (1890), is an outstanding analysis of species of Encalypta.

Structure of the peristome has long been considered important in classifications of the Musci because the structure tends to be stable within genera and even within families. As early as 1827, Nees, Hornschuch and Sturm recognized that peristome structure is actually variable within the genus Encalypta, as noted above. However, it was not until Philibert's (1884-1890) investigations of the relationship between peristome structure and the natural affinities of mosses that attention was drawn to the potential significance of the genus Encalypta relative to the phylogenetic inter-relationships among the major groups of the Musci. Philibert (1884) supported Mitten's (1859) division of the Musci (excluding Sphagnum and Andreaea) into two major groups based on fundamental differences in the peristome structure. The Nematodonteae, comprised of the

Polytrichaceae, were characterized by each peristome tooth being composed of a number of simple filaments joined laterally, while the Arthrodonteae, which consisted of all other mosses, were characterized by the peristome being composed of teeth with transverse articulations. Philibert also placed the Tetraphidaceae in the Nematodonteae in agreement with Lindberg's observation that the teeth of *Tetraphis* resemble those of *Polytrichum* and are not truly analogous to those of other mosses. In addition, Philibert recognized two 'extreme and opposite' peristome-types within the Arthrodonteae. The Diplolepideae included mosses with the outer peristome characterized by "...une double série de plaques extérieures et une seule série interne;...", while the Aplolepideae [=Haplolepideae] included those with the opposite condition, that is, "...la rangée externe qui est simple, la série étant alors presque toujours double.". Philibert then presented an overview placing most genera of mosses into one or the other group; however, he did not include the Encalyptaceae in either the Diplolepideae or the Aplolepideae. Philibert regarded the Encalyptaceae as a "famille véritablement ambigue, et placée au point de séparation de toutes les autres.". He reported that the double peristome of *E. procera* and *E. streptocarpa* has the essential characters of the Diplolepideae, that the single peristome of *E. ciliata* and *E. rhaptocarpa*, and the more-or-less reduced form in *E. vulgaris* and *E. commutata* [=*E. alpina*] approach those of certain species of haplolepideae, and finally that in *E. longicolla* and *E. brevicolla* there are filamentous teeth that are "...plus analogues à celles des Polytrichs qu'à celles des Arthrodontées.". In later articles, Philibert (1889) described, in considerable detail, the structure of the peristomes of *E. longicolla*, *E. brevicolla*, *E. affinis* as (*E. apophysata*), *E. procera*, *E. streptocarpa* and *E. ciliata* in considerable detail. Although Philibert (1884) regarded the Encalyptaceae as the axial group from which other mosses diverged, he stated that without data from the fossil record it would be impossible to know whether the Encalyptaceae existed first or if the Polytrichaceae were the progenitors of the Encalyptaceae with the two groups of Arthrodontous mosses subsequently evolving from *Encalypta*.

Philibert's (1884, 1889) concept of the Encalyptaceae as the group of mosses that form the transition between the Nematodonteae and the Arthrodonteae has generally not been accepted. On the other hand, his ideas that both haplolepideous and diplolepideous peristome-types occur in the Encalyptaceae and that this family might, therefore, represent a transition between these two types has been given more credence. The influence of these latter ideas are reflected in Fleischer's (1904) historically important classification of the Musci, in which he placed the Encalyptaceae in a new subgroup, the Heterolepideae, between the Haplolepideae and Diplolepideae in the Arthrodontei. In Fleischer's (1904) classification, the Bryales consist of three suborders, the Arthrodontei, the Amphodontei and the Archidontei. Therefore, the Encalyptaceae are not placed in the ultimate central position suggested by Philibert (1884-1890). Furthermore, Fleischer (1904) made it clear that he did not accept Philibert's suggestion of a fundamental similarity in the peristome-type of E. longicolla and that of Buxbaumia in his circumscription of the Heterolepideae as "Peristomzähne entweder nach dem Typus der Haplolepideae oder der Diplolepideae gebildet, oder das opponirende innere Peristom mit dem ausseren verwachsen.". Fleischer also stressed that the unique calyptra of Encalypta is a vegetative feature that also warrants a special position in the system of classification. Earlier, Limpricht (1890) had also been critical of the suggestion of relations between Encalypta, and Polytrichum, Tetraphis and Buxbaumia, and pointed out that it presented no problem to derive the peristome of E. longicolla through fusion of the outer and inner peristomes. Dixon (1932) followed Fleischer and placed the Encalyptaceae in the subgroup Heterolepideae but he emphatically stated that Encalypta cannot be regarded as the ancestor from which both the Haplolepideae and Diplolepideae evolved. However, Dixon did suggest that the reduction of the peristome in Encalypta might serve as a model for understanding the evolution of the haplolepideous peristome: "...it is nonetheless probably true that all types of peristome within the genus are derived by reduction from a common ancestor having a double peristome, and that thus we have before us a perfectly close parallel, though a parallel only, to the more general reduction of the Haplolepideoid peristome.". Flowers (1938) considered the Encalyptaceae to form "...a transitional group between the Aplolepideae and Diplolepideae...showing the characteristics common to both.". Grout (1904) appears to have been the only person to fully support Philibert. On the basis of his own observations of peristome structure, Grout enthusiastically endorsed Philibert's theory. Grout concluded "My studies on the peristome have convinced me that the following arrangement of families would more truly represent the order of evolution than that one that I have previously followed:

Georgiaceae [=Tetraphidaceae], Polytrichaceae, Buxbaumiaceae, Encalyptaceae, Tortulaceae, Ephemeraceae, Grimmiaceae, Dicranaceae, Fissidentaceae.".

Recently, Edwards (1979) assessed the peristome-types that occur in some groups of haplolepideous and diplolepideous mosses. He was particularly concerned with the number of cell plates that occur on either surface of a peristome tooth. The results of Edwards' studies indicate that the five haplolepideous orders of mosses are characterized by a particular pattern that does not occur in other groups he studied. In a peristome that consists of 16 teeth, every group of two teeth has two cell plates on the outer surface (that is, each tooth consists of one) and three cell plates on the inner surface (that is, each tooth consists of one and one-half). He called this a 2:3 pattern. Edwards found no sign of the haplolepideous, 2:3 pattern in the species of Encalypta that he studied.

While the variation in peristome-types within Encalypta has long been remarked upon, until recently there has been very little mention of a parallel diversity in the structure of spores, although differences were recorded in descriptions as early as 1838 (Bruch, Schimper & Gümbel 1838). Vitt and Hamilton (1974) illustrated with scanning electron micrographs the superficial structure of spores of nine different species of Encalyptaceae. They recognized three major groups of species and suggested that these correspond closely to those proposed by Philibert (1889) on the basis of peristome structure. Vitt and Hamilton placed E. longicolla in a separate group because the spores were found to be extremely large, uniformly papillose and indistinctly polarized, while the peristome was reported to be composed of bundles of articulated whole cells in several radial layers with no differentiation of exostome and endostome. In the second group of species, the spores were considered to have relatively smooth papillae and little or no polarity, and the peristomes were described as all consisting of two layers with at least the inner layer composed of cell walls. The third group consisted of species with spores considered to be distinctly polarized, and, if present, the papillae "...possess either 'warts' or branches.". Peristomes in this group were reported to be either single or absent.

Járai-Komlódi and Orbán (1975) independently conducted a study similar to that of Vitt and Hamilton (1974) on nine species of Encalypta, eight of which had also been studied by Vitt and Hamilton. Járai-Komlódi and Orbán included both SEM's and light micrographs of acetolyzed spores. They too recognized three different spore-types, but the species were grouped "...according to certain principles of spore morphology." and they did not attempt to correlate these groupings with any other structural feature. Encalypta ciliata was placed in a separate group because they considered the structure on both faces of the spore to be very distinctive with a "...central brochus, the well-developed murus-like arms, the marginal meshes and the trilete mark which is most of all developed here.". The second group of species were placed together in recognition of similarities in ornamentation and the "cryptotrilete" aperture, but they also reported that the species in this group can also be well separated on the basis of some features and noted that E. longicolla differs from all species they investigated on the basis of the very large spores. The third group of species is comprised of those they considered to have apolar, katalept (that is, having a thin, more-or-less aperture-like . area on the proximal face (Erdtman 1965)) spores ornamented by granules, and they reported E. alpina to be somewhat transitional between the second and third groups because they found some differences between the two faces of its spores and considered the structure of the proximal face to be similar to that of E. longicolla. As Clarke (1979) noted, the species of Encalypta grouped together by Vitt and Hamilton (1974) are mostly different than those that Járai-Komlódi and Orbán (1975) grouped.

Fossil and Subfossil Remains of Encalyptaceae

There are no substantiated reports of pre-Quaternary fossil material of species of Encalyptaceae. Erdtman (1969) suggested that the Emphanisporites McGregor spores described from the Devonian of Canada (McGregor 1961) "...resemble...those of certain recent Encalypta species.". There are a number of records of subfossil specimens of Encalyptaceae. A few of these have been identified to species, but with the exception of Bryobrittonia and E. alpina, most Encalyptaceae are virtually impossible to differentiate on the basis of vegetative plants, although the choice can generally be narrowed to one or two species, or to a particular group (for example, the E. rhaptocarpa-E. vulgaris complex). Most of the subfossil material consists of vegetative plants or portions thereof, but a few specimens found recently include portions of calyptrae and important clues as to specific identify can be obtained from these in many instances.

Hesselbo (1910) included E. alpina in a list of species from a glacial deposit in Denmark; Janssens (1981) reported it from a Wisconsinian deposit in northwestern Yukon Territory (!) and from a deposit (dated at 6400 ±60 B.P.) on northern Ellesmere Island, Northwest Territories (!); and Miller has a specimen from the Columbia Bridge locality in upper Vermont (the vascular plants from this locality are reported in Miller and Thompson (1979)) from sediments dated at 11390 ±115 and 11540 ±110 B.P. (!). All of the above specimens consist of leaves and/or portions of stems with leaves, but there is also a calyptra fragment from the Columbia Bridge locality that is tentatively assignable to E. alpina. The first report of a subfossil specimen of B. longipes (Janssens 1981) is based on a specimen from a deposit (dated at 6200 ±120 B.P.) in the Anaktuvuk Valley in the Brooks Range of Alaska(!).

There are also reports of several other species of Encalyptaceae. Miller (1976) cited E. procera, on the basis of leaf and stem fragments, from the Two Creeks Forest Bed in eastern Wisconsin (dated at 11850 B.P.) and Janssens (1981) tentatively listed it from northern Ellesmere Island, Northwest Territories (!). I have seen a specimen from the Columbia Bridge locality (see above) that might be E. procera. Dickson (1973) reported several specimens of E. rhaptocarpa from the British Isles (Devensian deposits - 10270 ±170 to 19500 ±650 B.P.), including sporophytic material, and Janssens (1981) tentatively reported it from a deposit (11050 ±130 B.P.) in St. Eugene, Quebec (!). Some other material from the Columbia Bridge locality might belong to the E. rhaptocarpa-E. vulgaris complex(!). Dickson (1973) suggested that an undetermined specimen from Great Britain might be E. mutica, but I believe it is more likely that this sterile specimen represents E. procera(!). One of the specimens from the Columbia Bridge locality could be E. mutica, but E. procera cannot be ruled out with certainty (!). Abramova et al. (1965) tentatively identified E. vulgaris from an Upper Pleistocene deposit in Eastern Siberia on the basis of fragments that included spores, and a portion of a capsule and calyptra.

II. MATERIAL AND METHODS

Nomenclature: One of the important aspects of a taxonomic revision or monograph that markedly differentiates it from a floristic study is the nomenclatural treatment. The taxonomist must try to deal with all names legitimately proposed in the group being studied, and to establish the correct names for the taxa recognized in the treatment. I believe that the fundamental aim of the taxonomist should be nomenclatural stability. In my experience, this is usually possible within the guidelines of the International Code of Botanical Nomenclature (ICBN) (Stafleu et al. 1978).

There have been 87 specific and 72 subspecific (above the rank of forma) taxa validly published in the genus Encalypta; 16 specific and 11 subspecific taxa in the genus Leersia; and two species in the genus Bryobrittonia (based on Index Muscorum (van der Wijk et al. 1962, 1964, 1969) and my own records). Only those names above the level of forma are dealt with in the formal nomenclatural sections. The citations of sources of original descriptions are based upon those in Index Muscorum; however, mis-citations of page numbers, dates of publication and of authors have been corrected whenever they have come to my attention. Also, citations of journals are standardized according to Botanico-Periodicum-Huntianum (Lawrence et al. 1968), citations of authority names according to Sayre, Bonner and Culberson (1964), and recently published names not included in Index Muscorum (van der Wijk et al. 1962, 1964, 1969) or the Index Muscorum Supplementa (Crosby 1977, 1979) have been incorporated.

I have obtained and reviewed the original literature and protologues of all newly described names and new combinations, and the types of all basionyms have been examined, except in a very few cases when I have been unable to obtain specimens on loan or I have been unable to locate a type. (However, for E. rhaptocarpa, E. intermedia and E. vulgaris, the type of the basionym is indicated, but synonyms are not included. These will appear in a future publication devoted to elucidation of the taxonomic problems that centre around these three taxa.) I feel that it is important to make clear the basis for selecting a particular specimen to serve as the type. Therefore, the citation of the specimen(s) is quoted directly from the original publication first. This is followed by an indication that a holotype has been designated or a lectotype selected and the label information from that specimen is quoted directly for purposes of comparison with that cited from the original publication. Specimens have been typified in the context of the historical and current taxonomic concepts of each taxon so as to retain continuity whenever possible. In some instances, for example that with *E. affinis*, a careful evaluation of the protologue in relation to material in the author's herbarium has also been necessary (Horton 1981a). Typification of a name is generally an involved, time-consuming task, even in instances that appear superficially straightforward. In some situations, the original author's herbarium has been destroyed, for example Carl Müller's herbarium in Berlin, and a lectotype must be selected elsewhere. However, it is often possible to lectotypify material that was seen by the original author. For example, it is known that Müller exchanged specimens with Kindberg, Brotherus and Levier; therefore, potential types exist in S, H and FI, among other places.

Recently, it has been suggested that types of specimens described prior to establishment of the type-concept (*sensu* N. L. Britton) in the 20th century cannot be designated as holotypes, even if only one specimen is cited in the original publication (Guédès 1978). It is Guédès' contention that such specimens can only be lectotypified because the method was unknown at the time they were designated. However, both E. G. Voss and P. Isoviita have pointed out (*in litt.*) that such a statement represents a misinterpretation of the ICBN. A holotype is defined in Article 7.3 (Stafleu *et al.* 1978) as "...the one specimen or other element used by the author *or* [my italics] designated by him as the nomenclatural type."; therefore, if there is reasonable certainty that an author based his description on a single specimen, that specimen may correctly be designated a holotype. I agree with Isoviita (*in litt.*) that the specimen extant in the herbarium of the original author should not automatically be considered a holotype, particularly if duplicates exist in other herbaria. A lectotype should be selected, unless there is some way to be sure that the description is based upon only one of the duplicates. Vitt (1980) has recently pointed out that the designation isolectotype, which is not included in the ICBN, can give a misleading status to a specimen. Therefore, that term is not used in the present study.

In the Encalyptaceae, there are two instances of orthographic inconsistencies in the citation of particular names. The epithets *longicolla* and *brevicolla* were originally published with a final "a" in the case of *E. longicolla* and *E. longicolla* var. *brevicolla* (Bruch, Schimper & Gümbel 1838). However, if Crundwell's (1970a) suggestion is followed, these epithets should be altered to *longicollis* and *brevicollis*. Recently, Crum, Steere and Anderson (1973) followed the original spelling and listed *E. longicolla* and *E. brevicolla* in their Checklist, as did Ireland *et al.* (1980), while Koponen, Isoviita and Lammes (1977) used the altered form of *E. brevicollis*. Crundwell stated, with reference to epithets formed from *collum*, that while -*collis* is the usual form, -*collus* (or the laternatives -*colla*, -*collum*) are not erroneous. However, he also stated that "Bryological practice should conform to that of biologists as a whole." and reported that epithets with any of the -*collus* forms virtually do not exist in either animals or phanerogams. Therefore, Crundwell concluded that bryophyte epithets ending in -*collus*, -*colla* or -*collum* should be emended to -*collis* or -*colle*.

It is stated in Article 23.5 of the ICBN (Stafleu *et al.* 1978) that "The specific epithet, when adjectival in form and not used as a substantive agrees grammatically with the generic name." and in Article 73 that "The original spelling of a name or epithet is to be retained, except for the correction of typographic or orthographic errors.". *Encalypta* is feminine (even though the Greek word that it is transliterated from is masculine); therefore, the endings -*colla* or -*collis* or their forms would be equally correct. As the original spellings were *longicolla* and *brevicolla*, it would be a direct contravention of the Code to change these epithets as Crundwell (1970a) has proposed. In the present treatment, *E. longicolla* and *E. brevicolla* are used.

The other instance concerns *E. rhaptocarpa*, as it was originally spelled (Schwaegrichen 1811), or *E. rhabdocarpa*, as it has been cited in many later treatments. As far as I have been able to determine, this change was initiated by Bruch, Schimper and Gümbel (1838); such earlier authors as Bridel (1819, 1826), and Nees, Hornschuch and Sturm (1827) were consistent with the original author's spelling. Although Bruch, Schimper and Gümbel gave no reason for the change, it is quite clear that it was intentional as they stated in the introduction to *Encalypta* "C'est BRIDEL qui, dans sa *Muscologia recentiorum*, fait le premier mention de *l'E. rhabdocarpa* (et non *rhaptocarpa*)...". Many later authors have followed Bruch, Schimper and Gümbel, including Müller (1848-1849), De Notaris (1869), Schimper (1876), Limpricht (1890), Brotherus

(1902, 1924), Coker (1918) and Flowers (1938), and most recently Nyholm (1954), Savicz-Ljubitskaja and Smirnova (1970) and Lawton (1971). In contrast, Crum, Steere and Anderson (1973) listed *E. rhaptocarpa*, and Crum (1973) noted the discrepancy between the original spelling and that used by many later authors. He quite correctly pointed out that "...the original spelling in Schwaegrichen's herbarium and in his publication was *rhaptocarpa*".

Article 73.1 of the ICBN also applies in this instance, that is, the original spelling should be followed unless there is a typographic or orthographic error. However, "...Article 73 and its associated recommendations is not one of the more definite parts of the ICBN..." (Wilbur 1981) and interpretations of what constitutes an orthographic error vary considerably. For example, Hickman and Vitt (1973) argued that the original spelling of *Weissia waymouthii* Brown should be retained even though Brown had stated that the species was named after Mr. Waymouth, whose name was actually spelled Weymouth. Wilbur (1981) is of the opposite opinion in a similar situation. He reported that Oersted published the generic name *Oreomunnea* Oerst. stating that it was in honor of Francisco Oreomunna; however, Oersted apparently discovered later that the name of the person in question was actually Oreamuno and altered the genus to *Oreamunoa*. Wilbur concluded that Oersted was mistaken in his spelling of the family name and that the correct orthography is *Oreamunoa*. As stated above, I feel that nomenclatural stability should be a primary objective of taxonomists; therefore, whenever possible the original author's spelling should be retained. The situation with *Oreamunoa* may be an exception where the alteration should be accepted since the original author made the correction.

In the instance of the spelling of the epithet *rhaptocarpa* the situation is more clear-cut than in the examples cited above. There is no concrete evidence that the original spelling is in error. First of all, it clearly is not a typographic error because Schwaegrichen wrote the name on the type specimen as well as publishing it. I suspect that it has been regarded as an orthographic error. There are two Greek words, transliterated as "rhabdo" and "rhapto", that obviously are very similar orthographically. According to the Greek-English Lexicon (Liddell & Scott 1961), the first means striped or streaked and the second means strung together, united, woven or sewn together. As "carpa" means fruit and Schwaegrichen described the theca of *E. rhaptocarpa* as having linear, red ribs, it is very likely that he had the meaning of the first word in mind, but used the second. Dr. R. C. Smith of the Department of Classics, University of Alberta, has pointed out (pers. comm.) that the combination of letters transliterated as "pt" is far more common than the "bd" combination. Therefore, it is probable that Schwaegrichen was more familiar with the former. However, in the original description (Schwaegrichen 1811) there is no indication of the origin of the epithet nor of its meaning. There is no direct evidence that E. rhaptocarpa is an orthographic error. Such a conclusion can only be based upon supposition. Therefore, I think that the epithet should be accepted as Schwaegrichen originally wrote it.

Taxonomic Concepts: Attempts to define what a species is have been the source of considerable controversy, and copious literature has been devoted to this subject as a result. Basically, there are three concepts of what constitutes a species, these being the taxonomic, the biological and the evolutionary concepts, none of which has proven to be universally acceptable. Reviews of these concepts are in Davis and Heywood (1963), Grant (1971), Løvtrop (1979), Mayr (1969), Raven (1976), Simpson (1961), Sneath and Sokal (1973) and Sokal (1973).

The taxonomic or phenetic species concept is based on observations of structural resemblances and differences. A species is considered to consist of individuals that are more-or-less alike structurally and are differentiated from other such individuals by structural gaps or discontinuities. Undoubtedly this has been and still is the most widely applied concept when it comes to classifying plants and animals. One of the major criticisms levelled at the taxonomic concept is that it is highly subjective and arbitrary, although it has been argued that the application of numerical techniques of analysis will aleviate these problems (Sneath & Sokal 1973). Also, it has been suggested that the taxonomic concept is non-biological or typological. However, the latter commonly represents a misunderstanding of the nomenclatural requirement for a type specimen of each species. The type is a representative specimen only in the nomenclatural sense; it may or may not be representative in the taxonomic sense.

The biological species concept is essentially a genetic concept (Simpson 1961). It is generally attributed to Mayr (1963) who modified his original definition and stated that

"Species are groups of interbreeding natural populations that are reproductively isolated from other such groups." (Mayr 1969), although this general idea is apparent in early biological literature (Raven 1976). This definition can be seen to have general applicability, at least in theory, to animals, although the inability to demonstrate that interpopulational gene flow is a reality is a major difficulty. Furthermore, it has been suggested that selective pressures, not gene flow, are perhaps the more important unifying force between populations (Ehrlich & Raven 1969). The biological species concept has been more difficult to apply to plants because of some reproductive characteristics that are particularly prevalent in this group of organisms. Raven (1976) discussed the occurrence of hybridization in natural populations of Angiosperms and pointed out that selective pressures may favor the lack of interspecific reproductive barriers in woody plants. Also, there are many plants that reproduce exclusively uniparentally or vegetatively. Under the biological species concept such plants cannot be regarded as species even though they may be well-defined entities structurally.

The evolutionary species concept was defined by Simpson (1961) as "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies.", but the general idea of continuity of species through time has a long history in the literature (Grant 1971). Recently, Wiley (1978) has proposed a modified version of Simpson's evolutionary species concept that incorporates the view propounded by Ghiselin (1974) that species are individuals just as organisms are and that they are not just a construct of the human mind. The evolutionary species concept encompasses both the taxonomic and biological concepts, and has the advantage over the latter that it includes uniparental or asexually reproducing organisms.

Anderson (1963) discussed some of the problems in the application of "modern" or biological species concepts to mosses. He concluded that they "...roughly parallel those [encountered] in other plants.". Data suggest that gene flow distances in mosses are exceedingly short (Anderson & Lemmon 1974, Bedford 1938). Furthermore, many mosses reproduce sexually very seldom (Anderson 1963) and among those that do many are autoicous and therefore probably inbreeders. In the Encalyptaceae, all except two species are autoicous. Of the two dioicous species, very few populations of

Bryobrittonia have been found with sporophytes and it seems likely that most propagation of this species is vegetative. At best, the biological species concept is difficult to apply to mosses in general and to the Encalyptaceae in particular, at least in a functional way.

I believe that any sound systematic treatment must be based upon thorough, detailed knowledge of the structure of the taxa, which can only be attained through an extensive and intensive study of herbarium specimens. Raven (1976) has gone so far as to suggest that data obtained from populational studies of cytology, chemistry and ecology, among others, should not be incorporated into a classification. Rather these kinds of studies should be considered as separate from the study of organisms for classification purposes (Raven 1976). However, such studies provide useful information and evidence supportive of conclusions based on structure, in some instances, and may provide additional insight when the structural information is ambiguous. Also, a full understanding of any group of organisms can only be achieved by co-ordinating field studies with the herbarium studies (Schuster 1966). Not only does this approach place the group being studied into perspective in relation to other components of the vegetation, but most importantly, it gives a populational perspective to the herbarium work. Therefore, I feel that such "biological" information should be incorporated whenever possible, but not to the point of exclusion of, or priority over, structural data.

I consider myself to be a systematist, as opposed to a taxonomist, in the sense that I deal not only with the delimitation of taxa in order to facilitate identification, but also with defining the phylogenetic or evolutionary relationships among these taxa. This latter, more theoretical aspect of my treatment is founded in the belief that species are not just convenient constructs that taxonomists create for purposes of classification, but that they have some reality just as an organism does. However, most species presumably exist for much longer periods of time than the individuals and populations of which they are composed and it is the recognition of this time element, the belief that species have some continuity through time, that is crucial for phylogenetic reconstruction. It seems plausible to suggest that there must be some genetic interchange for a species to maintain its continuity and that there must be a lack of such interchange, or a lack of effective (in an evolutionary sense) interchange, with other species for each to have a unique evolutionary history. However, events of genetic interchange between populations of a single species may be far less frequent than has previously been thought, at least in some groups of organisms, but such other factors as selective forces may be equally effective in maintaining continuity. Therefore, my species concept is an evolutionary one with a strong emphasis on structure as the basis for the taxonomic and evolutionary conclusions drawn.

As with species concepts, infraspecific categories have been a source of confusion and controversy. The individual categories have been, and still are, applied in diverse ways (see Lawrence (1951) for a review). There have been objections to giving formal nomenclatural recognition to infraspecific categories (Simpson 1961) and the taxonomic value of some such categories has been questioned (Wilson & Brown 1953). Among the reviews of infraspecific categories, that in Mayr (1969), from a zoological perspective, and that in Davis and Heywood (1963), with a botanical outlook, are particularly lucid.

The three most common of the infraspecific categories are subspecies, variety and form. The subspecies has been widely utilized by zoologists (Mayr 1969), but has received less acceptance from botanists (Davis & Heywood 1963). Subspecies generally have been defined as variants of the species that differ consistently in one or several character-states and inhabit a broad geographic subdivision of the range of that species. In botany, this subspecies concept is generally attributed to Du Rietz (1930) and Rothmaler (1944, 1954 and 1955). Some of the practical problems associated with the subspecies concept outlined above are exposed by Wilson and Brown (1953), but the subspecies category is defended by Smith and White (1956), among others. Simpson (1961) pointed out that the concepts of subspecies as "little species" or "incipient" species represent misunderstandings of the purpose of this category. He stated emphatically that "They [subspecies] are taxa of a markedly different kind from species, and relatively few of them will ever become species...". Simpson (1961) described subspecies as "...formal taxonomic population units,...". With reference to bryophytes, Crundwell (1970b) suggested that the subspecies category could be better used to provide meaningful groupings of varieties when several occur within a single species.

The category of variety has seldom been used by zoologists (the subspecies is the only infraspecific category recognized in the International Code of Zoological Nomenclature (Stoll et al. (1961)) and Mayr (1969) attributed this to Linnaeus' use of the term to describe any variant from the type (in a typological, pre-evolutionary sense) of the species. On the other hand, the variety has been widely employed by botanists, and Davis and Heywood (1963) suggested that the fact that Linnaeus used the term has given it credibility. Generally, the variety has been used to describe structural variants that occupy a restricted geographical area within the range of the species. Therefore, the primary difference between subspecies and varieties is one of geographical extent, and Davis and Heywood (1963) pointed out that "...subspecies may differ from one another in fewer and less well-marked characters than varieties or even forms within the same species.". Bryologists have widely used the category of variety to circumscribe ecological modifications.

Most botanists consider forms to be sporadically occurring variants that have a genetic basis (Lawrence 1951). However, among bryologists the category has been widely applied to ecological variants (see Podpěra 1954, for example).

There seems to be general agreement that one or two infraspecific categories are sufficient for formal nomenclatural recognition. Zoologists tend to use only the subspecies (Mayr 1969, Simpson 1961), while botanists use both subspecies and variety (Davis & Heywood 1963). The subspecies category has been used infrequently in bryology by comparison to the variety. Crundwell (1970b) reported a trend among bryologists in recent years to disregard infraspecific categories. He advocated their use because they focus attention on and stimulate investigation of variation that might have biological significance and could otherwise be overlooked.

In this study of the Encalyptaceae, my concepts of subspecies and varieties are the geographical ones, as outlined above. I have also found the idea that subspecies are not necessarily more markedly differentiated structurally than varieties (Davis & Heywood 1963) to make these concepts more workable in the group with which I am dealing. I regard forms as ecological modifications and these are given no formal taxonomic recognition.

Descriptions: The descriptions and the discussions of diagnostic and differentiating features of each taxon are based upon examination of living material as well as dried herbarium specimens. The scope of this study is world-wide, particularly in the sense that the descriptions and, ultimately, the taxonomic concepts presented herein are based upon specimens representative of as many different geographical areas throughout the world as possible. Most species of Encalyptaceae have been personally collected in North America from Alaska to Mexico and eastward to Ontario and Michigan. Collections have also been made in Hawaii, the Peruvian Andes, the Swiss and Austrian Alps, central West Germany, southwestern and northern Sweden, and southern Finland. Representative herbarium specimens of all species historically or currently recognized in the genera Bryobrittonia, Encalypta and Leersia were examined. These specimens include all of those made available to me by the curators of the following herbaria: Priv. Herb. S. Agnew (Aberystywth), ALA, ALTA, ASU, B, Priv. Herb. J. Bartlett (Auckland), BC, BERN, BISH, BM, BP, CANM, CAS, CHR, Priv. Herb. S. P. Churchill (Lawrence), CM, COLO, Priv. Herb. A. C. Crundwell (Glasgow), DUKE, DUIS, E, EGR, F, FH, FI, FLAS, Priv. Herb. J.-P. Frahm (Duisburg), Priv. Herb. W. Frey (Giessen), G, GB, GJO, GL, GZU, H, Priv. Herb. J.-P. Hebrard (Marseille), Priv. Herb. P. & E. Hegewald (Niederzier), Priv. Herb. F. J. Hermann (Ft. Collins), HIRO, Priv. Herb. W. J. Hoe (Honolulu), Priv. Herb. D. G. Horton (Edmonton), HSC, IRK, JE, KRAM, Priv. Herb. H. Kürschner (Tubingen), L, LAU, M, MICH, MIN, MO, MSC, NAM, NEB, NFLD, NICH, NY, O, PC, PE, PLZ, Priv. Herb. J. Poelt (Graz), PRC, QFA, RO, S, SMU, Priv. Herb. N. Takaki (Hiroshima), TENN, Priv. Herb. C. C. Townsend (London), TRH, TUR, UAC, UBC, UC, US, UWSP, Priv. Herb. J. Váňa (Prague), W, WIS, WTU, Z. Specimens were also requested from C, Dushanbe, LE and Shenyang, but these have not been made available to me. The herbarium abbreviations are standardized according to Index Herbariorum (Holmgren & Keuken 1974) and Bryological Herbaria (Iwatsuki, Vitt & Gradstein 1976).

Specimens were examined dry for determining habit of the leaves and seta, and shape of the capsule and calyptra. They were moistened in warm water for habit of the leaves, but shape of the capsule and calyptra was found not to differ significantly when moistened so this is not included in the descriptions. Measurements were made under the conditions outlined below with the characters in the order that they are dealt with in the descriptions. Measurements of overall plant length were from dry material under the stereoscope and include only the vegetative portion; of leaves were from moist material under the stereoscope and do not include such apical elaborations as a mucro or hair-point, or such a basal extension as a decurrent costa; of laminal cells were from moist material under the compound microscope and include only the lumina of upper cells, but in the basal cells include everything up to the middle lamella; of seta length were from dry material under the stereoscope from the point where the seta becomes visible above the leaves to the base of the capsule; of seta diameter were from moist material under the compound microscope; of capsules were on dry material under the stereoscope from the point where the seta begins to the capsule mouth; of peristomes were from dry material under the stereoscope from the rim of the capsule to the tip of the teeth; of exothecial and rim cells were from moist material under the compound microscope and include everything up to the middle lamella; of spores were from moist material under the compound microscope; and of calyptrae were from dry material under the stereoscope. The laminal and exothecial cells measured were chosen by scanning the material to get a feeling for the upper and lower size limits of the majority of cells. Representative cells were then measured to illustrate these upper and lower limits. The measurements in the descriptions represent what occurs in most cells of most populations; the bracketed measurements represent the more extreme upper and lower limits that occur in some populations.

I believe that the functional part of a taxonomic treatment, with respect to determination of specimens, should be those discussions under each species that are herein termed Diagnosis and Differentiation. In these discussions I have extrapolated from the descriptions all features that I feel are of value in identifying a particular species. In addition, there is a discussion of other species that might be confused with the one under consideration and how they can be most readily differentiated. This leads to the obvious question of whether formal descriptions have any purpose at all. In order to determine what the taxonomically significant features are, one must examine every possible structure and keep some sort of record of what is found with respect to individual species. I think that these 'records' or descriptions of all details studied should be included in revisionary treatments for several reasons. The description is a record of exactly which structures were studied, in others words, these are the data that the 'conclusions' or Diagnosis and Differentiation are based upon. The descriptions are a permanent record of the basis for the taxonomic conclusions. It is unfortunate that too many floristic and taxonomic treatments present only data. In some publications the features considered taxonomically important are italicized in the description; however, I feel that these features are better discussed as a coherent unit and in a more flowing style than is possible within the confines of a formal description. Also, further details of explanation can be added. Therefore, in the present treatment such basic structures as leaves, seta, spores and calyptra are italicized in the descriptions for ease of access to particular information. The more functional aspect of descriptions is that they serve as a reference for details not treated in Diagnosis and Differentiation.

Line Drawings and Scanning Electron Micrographs: Line drawings of a plant habit, capsules and calyptrae are based on dry specimens and were executed under a stereomicroscope with the aid of a drawing tube. Line drawings of leaves are based on thoroughly moistened material placed on a slide with the adaxial surface down and compressed under a cover slip. The drawings were done under a compound microscope with the aid of a drawing tube.

Scanning electron microscopy (SEM) is regarded not as a replacement for light microscopy, but as an aid to critical interpretation and as an effective mode for illustration of small and/or complex structures that do not lend themselves as well to interpretation by means of line drawings or words (Magill & Horton 1981). Specimens were studied first with a light microscope to select examples representative of the variation that characterizes a particular taxon. The selected material (except for brown spores) was then prepared for SEM in the following manner: (1) hydrated in distilled water, (2) sectioned freehand with a sharp razor blade (when applicable), (3) fixed in OsO_4 for two to twelve hours, (4) dehydrated through a 10, 20, 50, 75, 90, 95% sequence into 100% EtOH, (5) left in 100% EtOH overnight, (6) put through a 10, 20, 50, 75, 90, 95% sequence into 100% amyl acetate, and (7) left in 100% amyl acetate overnight. The material was then critical point dryed and mounted either on double-sided tape on stubs or in glue (Mikrostik) on stubs. Brown spores were mounted directly in glue on stubs with no prior preparation.

Cytology: For cytological analyses, material in meiotic condition was brought into the laboratory and kept in plastic bags at room temperature for up to a week until meiosis was detected. Slides were made from material fixed 2 to 3 minutes in Carnoy's Solution (1:3 acetic acid:95% EtOH) and stained with aceto-orcein or aceto-carmine. These were examined with the aid of Nomarski Interference Optics and photomicrographs were made. Unfortunately, the slides of _E. mutica_ and _E. longicolla_ were not preserved because at the time these were prepared I was unaware of the techniques for doing so. The slide of _E. affinis_ (in ALTA) was made permanent by freezing with CO_2 and mounting in Euparal according to instructions from H. P. Ramsay (_in litt._).

Habitat: The soil samples for the data presented in Figures 301-302 and Table 9 in the discussions of habitat for each of the species were collected with specimens of _Encalypta_ and _Bryobrittonia_, and air dried. For measurements of pH, the soil was passed through a two millimetre sieve and a one gram sample of the product was mixed with enough distilled water to make a slurry. This solution was the allowed to come to equilibrium for one-half to one hour at which point the pH was measured with a single probe (Beckman Electromate). For calculations of exchangeable cations (Ca^{++} and Mg^{++}) samples were prepared according to the NH_4OAc method outlined in Chapman (1965) and were then analyzed on an atomic absorption spectrophotometer at the University of Alberta.

As noted above, this treatment of the Encalyptaceae is based upon considerable experience with these plants as components of the vegetation in particular habitats and regions. However, the greater part of my field work has been carried out in North America and my familiarity with associated taxa is naturally better there than elsewhere. Therefore, the treatments of Habitat are no doubt most accurate on this Continent. However, on the basis of my own limited experience in Europe and South America, and from information on herbarium labels, I feel confident that my discussions are a reasonably accurate representation for the majority of populations of each taxon on a world-wide scale.

Distribution: I have mapped in North America every taxon known to occur there and I believe that these maps represent virtually all of the information that is currently available on each taxon (as of July 1981), with the exception of some Greenland localities because C's specimens have not been made available to me. I have attempted to map as many of the taxa that occur in Europe as possible, but have found this to be a time-consuming task because of a basic lack of familiarity with place names compounded by problems of illegible handwriting and languages in which I have little, if any, proficiency. Therefore, the time constraints have limited me to mapping only the scarcer taxa. A polar projection of those that occur in both North America and Europe or Eurasia is included. The gaps in the Asian portion of the polar projections are almost certainly artificial, but I have no way of knowing whether they represent disjunct collecting localities or if the maps would be much more complete if the specimens I requested from Dushanbe, LE and Shenyang had been made available. Those taxa that are endemic to South America are mapped.

Specimens Examined: Citations of specimens examined can be considered worthwhile for several reasons. They can be used to document the localities indicated on distribution maps, particularly disjunctions or edges of a range. Such documentation makes it possible to check the placement of a particular dot or to locate the specimen on which a record is based in order to check its identity. Secondly, lists of specimens give some indication of the total number of specimens of each taxon that were examined and upon which the description is based. Finally, one can request a loan of one or more of the specimens cited in order to gain an understanding of the taxonomist's concept. However, I feel that none of these purposes, nor all of them collectively, is of sufficient importance to warrant the amount of space that specimen citations consume in a publication, to say nothing of the time involved in compiling such records. Therefore, after lengthy consideration I have decided not to include detailed records of representative specimens examined for each of the taxa included in this treatment. I have, however, tried to make some of the information available in a more concise manner by listing for each taxon the number of specimens examined and annotated in each herbarium (numbers above 20 are rounded off to the nearest five). In total, over 10,000 specimens have been annotated.

III. TAXONOMIC TREATMENT

Structure

Overview: The most distinctive feature of the Encalyptaceae is the long-campanulate, mitrate calyptra that extends at least to the base of the capsule. Species of Encalyptaceae are predominantly autoicous and populations generally consist of plants covered by a mass of sporophytes. The cylindric capsule is exserted, but the seta is very variable in length. The family is noted for the diversity of peristome-types that characterize the different species, including those that are long and double, shorter and single or completely lacking. Vegetatively, the plants have a pottiaceous appearance. The leaves are quite broad and oblong with a well-developed, single costa. The upper laminal cells are more-or-less isodiametric, bulging, and, in all except one species, densely papillose. The strikingly differentiated basal cells are considerably larger and oblong with smooth walls, except for one species with the walls papillose on one surface. In most species the transverse walls of the basal cells are thickened and more-or-less intensely colored.

Habit: Plants of Encalyptaceae are acrocarpous. They grow erect; however, the production of the terminal sporophyte does not terminate growth of the plant. A subterminal innovation is subsequently produced and this becomes the main stem of the plant until it too is terminated by a sporophyte and the whole cycle is repeated. Therefore, the main stem is branched monopodially. Additional lateral branches are produced in all species of Encalypta, but not in Bryobrittonia, apparently independently of the production of a sporophyte, and these lateral branches also function as main stems with terminal sporophytes and subterminal innovations. Therefore, plants of species of Encalypta are more-or-less branched and appear quite dense, while those of Bryobrittonia consist of a single stem.

The length of the vegetative plants of Encalyptaceae, some of which exceed 40 millimetres, is not a very accurate indication of their size (as with most bryophytes); for the most part length reflects longevity. Judging by the considerable length of plants of some species of *Encalypta*, they may well live from ten to twenty years. Plants of *Bryobrittonia* do not seem to be as long-lived, perhaps enduring up to a maximum of five years. Size of plants of Encalyptaceae is most accurately estimated from the length of the leaves. By comparison to other Northern Hemisphere, acrocarpous mosses the plants are of moderate to small size. A generalization is that they are smaller than most species of *Dicranum*, larger than most species of Trichostomoideae and very similar in size to such Pottioideae as *Tortula* and *Desmatodon* species. However, within the Encalyptaceae there is considerable variation in size of different species. The largest have leaves as long as six or eight millimetres, while those of the smallest species are only up to two or three millimetres long.

The overall color impression is a very important feature that defines plants of many species of Encalyptaceae. Coloration of the leaves, costa, seta, capsule, peristome (when present) and calyptra blend and impart particular tones that, in some cases, are so striking as to make positive identification possible without the aid of any magnifying device.

Stem: In species of Encalyptaceae, the stem is more-or-less round in transverse section and the constituent cells are differentiated into two or three types. Plants of all species of Encalyptaceae have an epidermal and a cortical layer. The epidermis consists of one to three layers of cells that are more-or-less equal in size, but are smaller and the dark-orange walls are thicker than those of the cortical cells. Most of the stem consists of cortical cells that are parenchymatous in shape and rather irregular in size. The walls are thin with slight corner thickenings and yellow or orange. A distinct central strand of very small, thin-walled, parenchymatous and hyaline cells (Fig. 1) is always present in some species, but in others the central strand is indistinct or undifferentiated (Fig. 2). In older portions of the stem all of the cell walls are generally more darkly colored and thicker than in the distal younger parts.

Asexual Reproductive Structures: Specialized asexual reproductive bodies occur in two species of Encalyptaceae, *E. streptocarpa* and *E. procera*. Flowers (1938) stated that "Brood bodies have been observed in nearly every species, [of *Encalypta*] especially

Figures 1-4. Anatomy of Stem; Asexual Reproductive Structures.

Figs. 1 & 2. Transverse Sections of Stem. Scale=100 µm.

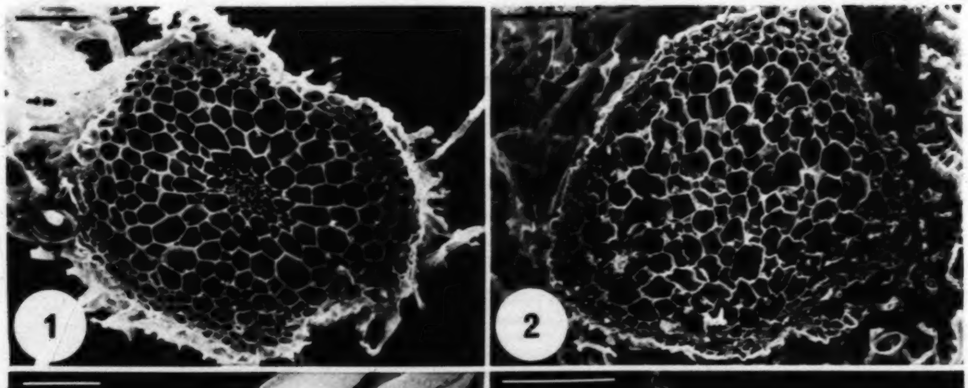
Fig. 1. *Bryobrittonia longipes*. Note central strand.

Fig. 2. *Encalypta ciliata*.

Figs. 3 & 4. *Encalypta streptocarpa*. Brood bodies. Scale=400 µm.

Fig. 3. Brood bodies in axils of leaves of sterile plant.

Fig. 4. Brood bodies with lower stalk and profusely branched upper portion.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sterile plants of rather moist habitats.". On the basis of my study of many specimens of all species of *Encalypta*, I am unable to support this statement. As far as I have been able to determine, brood bodies as described below occur only in the two species cited above. Flowers described brood bodies as "...mostly oblong or filamentous, multiseptate, reddish-brown, borne in the axils or the bases of the leaves.". It is marginally possible that his definition includes those structures treated here as axillary hairs (see below) but I have never observed these to be anything but hyaline in color.

Correns (1899) suggested that brood bodies of *E. streptocarpa* (as *E. contorta*) are in many respects similar to those of *Bryum capillare* L. *ex* Hedw. He described those of *E. streptocarpa* and gave a detailed account of their developmental history. He also reported that brood bodies of *E. procera* are very similar to those of *E. streptocarpa*, but he had only seen one specimen of the former species and it appears from his description that the plants were not in the best condition. I have found the brood bodies of *E. streptocarpa* to be indistinguishable from those of *E. procera* and some of Correns' concepts are incorporated into the following description. More-or-less dense clusters of brood bodies occur in the axils of leaves (Fig. 3) generally on stems that lack sporophytes, although they are also found on the lower part of some plants with sporophytes. The brood bodies can be considered to consist of two parts, the brood bodies proper and the lower stalk to which they are attached (Fig. 4). The cells that comprise the stalk are rhizoid-like in character. They consist of unbranched, or at most once-branched, filaments of oblong cells with oblique walls. Up to ten or twelve filaments are joined laterally to form a uniseriate mat. The superficial walls are smooth and orange to hyaline. The brood bodies proper are a profusely branched mass of discrete filaments that develop from the upper part of the stalk. The short-oblong or quadrate cells are approximately as wide as they are high and the walls are perpendicular. The slightly roughened superficial walls are dark-brown and strongly thickened, although in some the longitudinal walls along one side of the filament are thin giving it an appearance (with light microscopy) reminiscent of the annulus of a leptosporangiate fern.

Correns (1899) reported protonema to develop from the apex and the base of brood bodies of *E. streptocarpa*. The brood bodies germinated only in light with the exclusion of carbonic acid from the medium. He also reported that Berggren had observed the germination of brood bodies of *E. procera* and furthermore that parts of leaves of this species easily develop protonema. Correns concluded from this that the monoicous species, *E. procera*, is better equipped for asexual reproduction than the closely related, dioicous species, *E. streptocarpa*. I, too, have observed brood bodies of *E. procera* to germinate and have found that they readily do so under conditions of indirect sunlight for approximately 12 hours alternated with 12 hours of darkness on a nutrient-free substrate of moistened, sterilized sand.

Axillary hairs: Saito (1975) drew attention to the need to differentiate between paraphyses, that is, those filamentous structures associated with antheridia, and cauline paraphysis-like structures, which he termed axillary hairs. He also reported paraphyses to be uniformly thick-walled and pale yellowish-brown, while axillary hairs were said to be distinguished by hyaline walls (although he did note that in some species one or two basal cells or in others the uppermost cells are brownish). In the Encalyptaceae, I have found the antheridial paraphyses to be hyaline and only the upper cell walls are thickened. Also, in some species of Encalyptaceae, I have observed cauline paraphysis-like structures, which accord with Saito's description of axillary hairs. In *Bryobrittonia* and *E. affinis* there occur along the stem and also attached to leaf bases, mats of unbranched, hyaline and thin-walled filaments that are up to two millimetres long. These filaments are joined laterally at the base and each uniseriate mat is enclosed in a gelatinous substance. While in some respects these structures (particularly the more-or-less unbranched, thin-walled stalk portion) are suggestive of the brood bodies in *E. streptocarpa* and *E. procera*, the walls of the axillary hairs are transverse, not oblique as they are in the stalk of the brood bodies.

Leaves: The leaves are spirally arranged around the stem in all species of Encalyptaceae, but they appear denser and the plants more luxuriant in some species. Possibly this reflects the larger size of the leaves of some species, but it may also be a function of a shorter phyllotaxis. When dry, the leaves clasp the stem slightly below and are erect-spread above with the apices more-or-less incurved and twisted. The laminae are incurved to conduplicate in most to more-or-less inrolled in a few taxa. The costa forms a more-or-less prominent keel on the abaxial surface of the leaf. There are specific differences in the degree of contortion of the leaves. In some species the leaves are only slightly twisted in the upper part, in others they are strongly and irregularly or quite regularly twisted. Moist leaves are erect-spread to recurved-spread with the laminae inflexed. The lower leaves on the stem tend to be smaller than the upper and the apex is muticous in many, even if the upper leaves are hair-pointed. Scale-leaves (Fig. 81) have been observed only in Bryobrittonia on the lower part of the subterminal innovations that develop below the perichaetia and perigonia. In the Encalyptaceae the width of the leaves, and particularly the length, are variable within individual species. This is particularly apparent in those that have longer leaves. For example, leaves of E. streptocarpa have been found to vary from three to eight millimetres. The leaves of most species are oblong (Fig. 7), narrowly ovate-oblong (Fig. 8), narrowly elliptic-oblong (Fig. 5) or narrowly obovate-oblong (Fig. 6) with the apex abruptly narrowed and broadly acute to rounded (Figs. 5-8). However, most populations of E. alpina have the leaf gradually tapered to a narrowly acute apex (Fig. 9). In the Encalyptaceae, the apex is muticous (Fig. 5), mucronate (Fig. 8), apiculate (Fig. 9) or hair-pointed (Fig. 7 - lower left), but the variation is interspecific, not intraspecific, in most cases. In E. affinis, there is intraspecific variation; however, this variation is not random and differences in structure of the leaf apex correlate with distinct geographical patterns of distribution. Color of the leaves is different in many species of Encalyptaceae and contributes to the overall color impression of the vegetative plants. Brown tones are dominant in one species, black in another, yellow in still another and so forth.

Leaf Margins: Almost all species in the Encalyptaceae have the margins entire (Fig. 22). Bryobrittonia is the sole representative with crenulate margins (Fig. 23). While the margins are either plane (Figs. 5, 9) or recurved (Figs. 6,8), this variation is generally interspecific, although there are a few exceptional instances where intraspecific variation occurs. The recurvature is from the narrowing of the apex nearly to the leaf base in some species; in others it is from the mid-point of the leaf to the point where the basal cells begin. In still others, the recurvature is less uniform within individual species. In some populations, the margins are intermittently recurved from the narrowing of the apex, but in others they

Figures 5-9. Variation in Leaf Shape. Scale=1 mm.

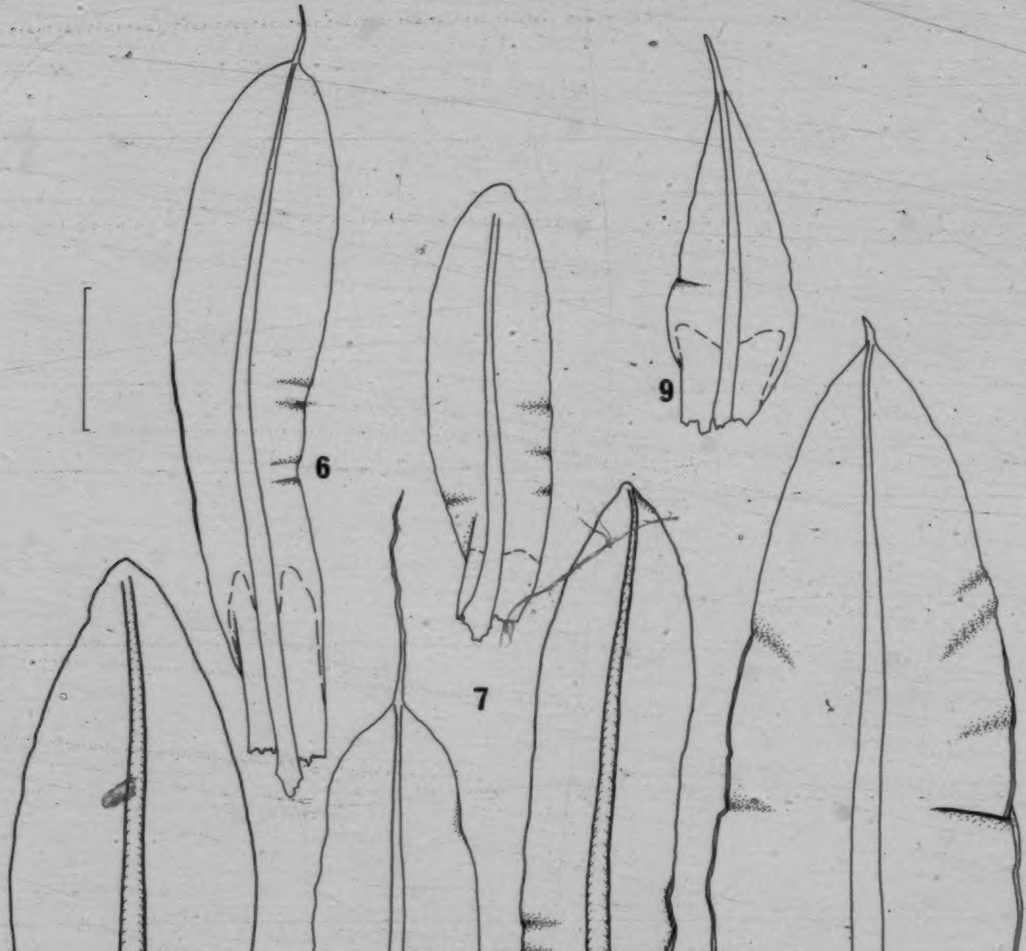
Fig. 5. *Bryobrittonia longipes*.

Fig. 6. *Encalypta affinis* subsp. *affinis*.

Fig. 7. (Clockwise from lower left) *Encalypta brevicolla*, *Encalypta mutica*, *Encalypta streptocarpa*.

Fig. 8. *Encalypta ciliata*.

Fig. 9. *Encalypta alpina*.



are recurved only in the mid-portion.

Costa: A strong, single, well-developed costa characterizes all species in the Encalyptaceae (Figs. 5-9). However, in different species and exceptionally within a single species, it is excurrent, percurrent, subpercurrent or ends well below the leaf apex (Figs. 5-9). Prominence of the costa on the abaxial surface varies interspecifically, for the most part, so that some species have strongly keeled leaves while others have a less distinct keel. The ornamentation and color of the abaxial surface are also important taxonomically. In some species the surface is perfectly smooth throughout (Fig. 12), in others it is quite densely papillose (Fig. 11) or it is smooth above (some have sparse, low scindulae distally) and densely papillose in specific areas below. The papillae on the costa are similar in structure to the laminal papillae (see below) or they are larger, "o"-shaped and more strongly branched with longer branches. In still other species there are short or, exceptionally, long, spinose projections (Fig. 13) instead of or in addition to papillae. These projections are simple (very few are branched apically) and hollow basipetally. A smooth costa appears very shiny under the stereoscope and papillose areas appear correspondingly dull. The color of the costa varies most interspecifically. It is green, yellow, golden, dark-red or dark-brown. In some species the color is quite different from the coloration of the laminae, in others it is very similar. In all Encalyptaceae, the adaxial surface of the costa is covered by laminal-type cells in the upper part (Fig. 10) and smooth below, approximately from the point where the transitional cells (see below) begin.

In transverse sections of the costa, there is an abaxial stereid band, but never an adaxial (Figs. 14-15). Brotherus (1924) reported the Encalyptaceae to have "...starkem dorsalen und Schwachem ventralen Stereidbande;..." and included a figure of a transverse section of E. streptocarpa taken from Limpricht (1890). In this figure, there are a few cells, just below the upper epidermis of laminal-type cells, that could be interpreted as stereids. I have observed such cells in transverse sections of species of Encalypta, although in my experience the lumina are not as small as those of the stereid bands on the abaxial surface, but are more like the laminal-type cells of the upper epidermis. Therefore, I would not consider this to be a second stereid band. In transverse section of

Figures 10-15. Structure of Costa.

Figs. 10 & 11. *Encalypta brevicolla*. Scale=40 μm.

Fig. 10. Adaxial surface.

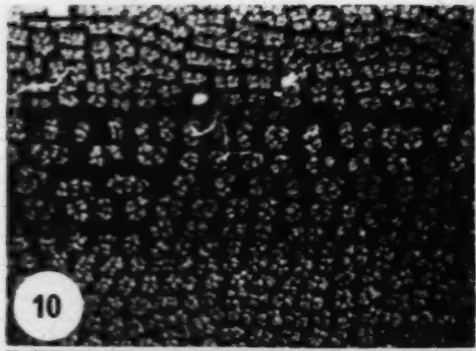
Fig. 11. Abaxial surface.

Fig. 12. *Encalypta microstoma*. Abaxial surface. Scale=40 μm.

Fig. 13. *Encalypta armata*. Abaxial surface. Scale=100 μm.

Fig. 14. *Encalypta microstoma*. Transverse section. Scale=40 μm.

Fig. 15. *Bryobrittonia longipes*. Transverse section. Note central group of begleiters. Scale=40 μm.



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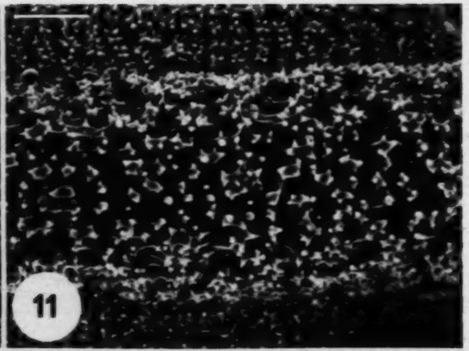

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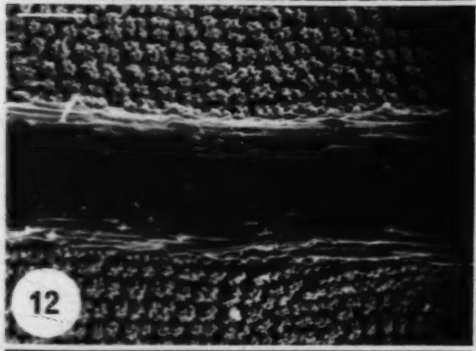

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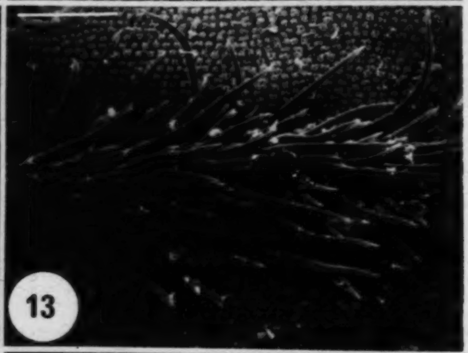

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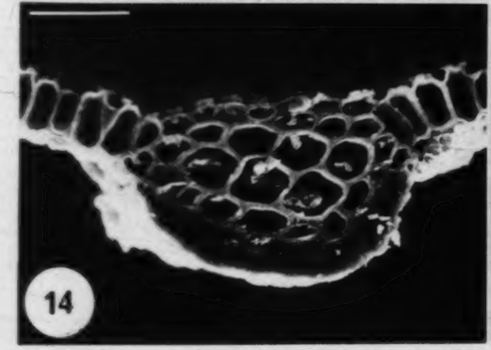

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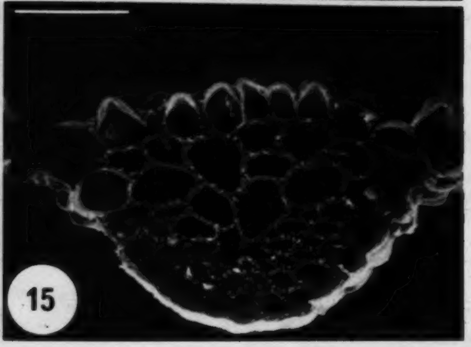

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the costa three or perhaps four different cell-types are recognizable in all species of Encalyptaceae (Figs. 14-15); in addition, begleiters are more-or-less differentiated in Bryobrittonia (Fig. 15) and a few species of Encalypta. Walls of all cells, except the begleiters, are evenly, more-or-less strongly thickened and the different cell-types are differentiated primarily by differences in size of the cell lumina. The epidermal cells on the adaxial surface are slightly smaller but otherwise undifferentiated from the laminal cells. Below the epidermal cells is a prominent cluster of ventral cells with large lumina. There are from two up to four or five rows of these cells and size of the lumina increases slightly towards the abaxial surface. The abaxial portion of the costa consists of from two to eight rows of stereids. One to two rows of abaxial epidermal cells are slightly enlarged in some. The variation in the number of stereid bands is taxonomically important and tends not to vary much intraspecifically. A small, central cluster of begleiters with minute or small lumina and very thin walls occur below the ventral cells, consistently in Bryobrittonia and sporadically in some species of Encalypta. In superficial view, the cells on the abaxial surface of the costa and on the lower part of the adaxial surface are short or long and narrowly-oblong. I have not found any taxonomically significant differences in the shape of these cells as Crundwell and Nyholm (1962) did with Tortella inclinata (Hedw. f.) Limpr.

Leaf Cells: All species of Encalyptaceae have unistratose laminae (Figs. 20-21). The upper laminal cells are more-or-less isodiametric to subquadrate or short-oblong and slightly angular with rounded corners (Figs. 16-19). In most species, they measure approximately 7-18 μm wide by 7-23 μm long, although they tend to be slightly smaller in some species. Those of Bryobrittonia are generally somewhat larger. The walls are thickened and they bulge prominently on both surfaces, but slightly less on the abaxial in many species (compare Figs. 16-17, 18-19). In Bryobrittonia, the walls are superficially smooth on the adaxial surface and smooth with a distinct contraction in the upper part on the abaxial (Figs. 18-19, 21). In contrast, the cell walls are not smooth in species of Encalypta, but are further elaborated by papillose protuberances on both surfaces (Figs. 16-17). Each papilla consists of a basal stem supporting a cluster of very short, digitate branches (Fig. 20). The cell lumin extends into the base of the papilla in some species and

Figures 16-21. Upper Laminal Cells of Encalypta and Bryobrittonia. Scale=10 μm.

Figs. 16–17. Encalypta ciliata.

Fig. 16. Abaxial surface.

Fig. 17. Adaxial surface.

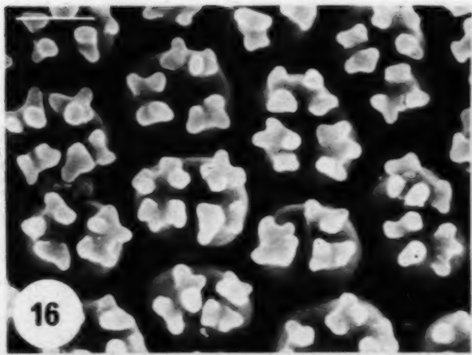
Figs. 18–19. Bryobrittonia longipes.

Fig. 18. Abaxial surface.

Fig. 19. Adaxial surface.

Fig. 20. Encalypta procera. Transverse section.

Fig. 21. Bryobrittonia longipes. Transverse section.



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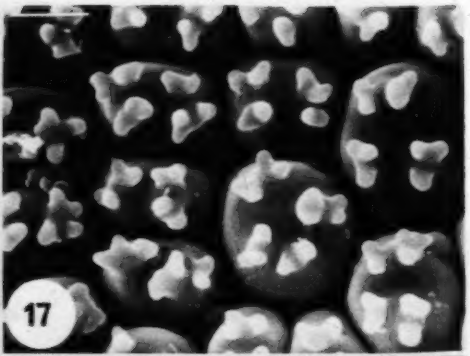

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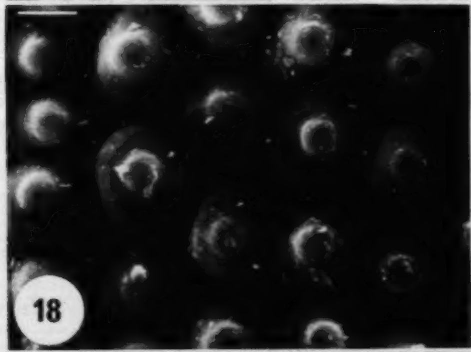

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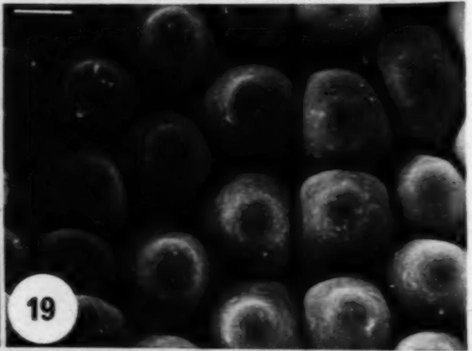

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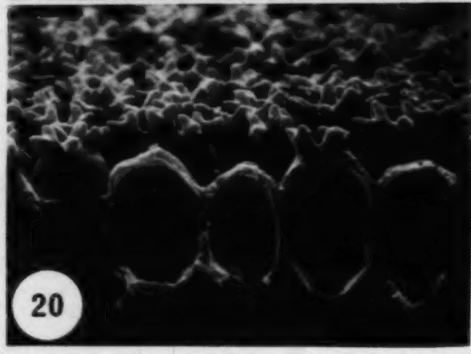

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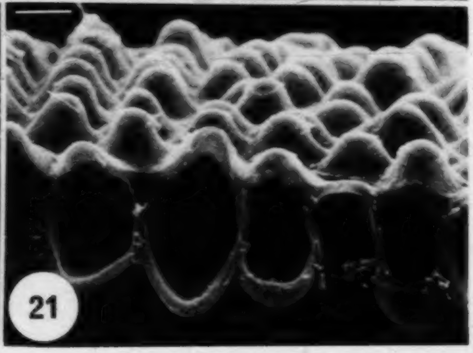

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not in others. In superficial view, the papillae are more-or-less "c"-shaped in some species, with short, knobby protuberances on the "c"; in others, there are just knobby protuberances and the "c" is less apparent. There are from two to six or eight papillae per cell and the variation is primarily intraspecific.

One to two rows of upper marginal cells are subtly differentiated in all species of Encalyptaceae. In species of Encalypta there is a single row and the lumina are ovate, with the narrow end positioned perpendicular to the margin, to subquadrate. The walls of these cells are strongly thickened so that the margins are entire (Fig. 22). In transverse section the walls are somewhat flattened, although they are papillose as the laminal cells. In Bryobrittonia, one marginal row of cells in the upper half of the leaf are skewed and more-or-less rhomboidal in shape with the upper corner free marginally (Fig. 23). This gives the crenulate appearance to the margin. In transverse section, the cell walls are smooth and more-or-less plane, except in the projecting corner where they bulge slightly on both surfaces. Below the mid-point of the leaf in Bryobrittonia, these marginal cells grade into one and then two rows of narrowly oblong cells that ultimately grade into the basal cells. Therefore the leaf margins are entire in approximately the lower half of the leaf. In transverse section the walls of these oblong, marginal cells are plane so that in superficial view under the stereoscope they are visible as a very narrow, shiny border.

In all species of Encalyptaceae, the enlarged, oblong basal cells are quite distinctly differentiated from the upper cells. This is most striking in the genus Encalypta because the smoothness of the basal cell walls (in all but one species) is a striking contrast to the strongly papillose upper cell walls. However, the transition to the basal cells, which occurs approximately two-thirds of the distance below the leaf apex, is relatively gradual in some species of Encalypta while it appears rather abrupt in others. This is an important taxonomic feature that is attributable to differences in ornamentation of the walls of this group of cells, which I term transitional cells. These cells are quadrate to oblong and more-or-less chlorophyllose. In surface view the walls are somewhat thickened and papillose above to more-or-less smooth basipetally. Structurally the papillae are like those on the upper cells or they are enlarged, "o"-shaped and much-branched with long branches. On the adaxial surface, the walls of the transitional cells in some species are, for the most part, plane and smooth, while the papillae extend

Figures 22-27. Upper Marginal Cells; Transitional Cells.

Figs. 22-23. Comparison of Leaf Margins of Encalypta and Bryobrittonia.

Fig. 22. Encalypta brevicolla. Note entire margin. Scale=20 μm.

Fig. 23. Bryobrittonia longipes. Note crenulate margin. Scale=10 μm.

Figs. 24-27. Variation in Transitional Cells of Species of Encalypta.

Figs. 24-25. Encalypta brevicolla.

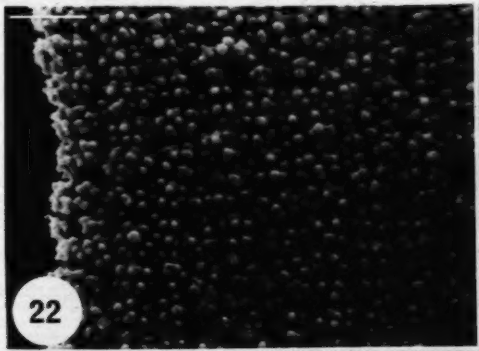
Fig. 24. Abaxial surface. Note that papillae extend to basal cells. Scale=100 μm.

Fig. 25. Adaxial surface. Note that papillae end well above basal cells. Scale=200 μm.

Figs. 26-27. Encalypta streptocarpa. Scale=100 μm.

Fig. 26. Abaxial surface. Note that papillae extend to basal cells.

Fig. 27. Adaxial surface. Note that papillae extend almost to basal cells.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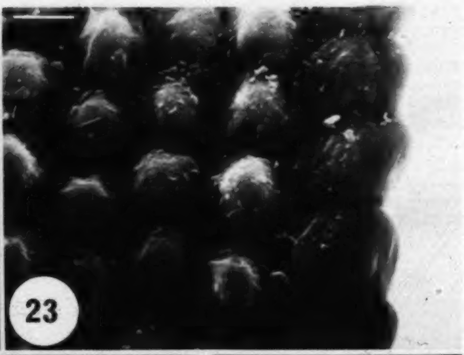
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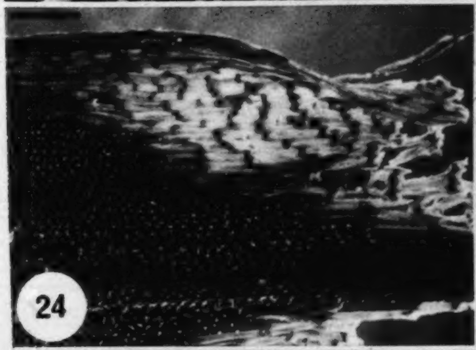
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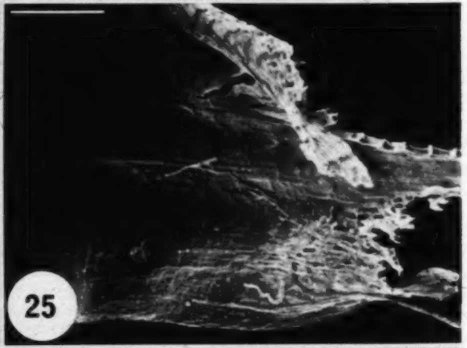
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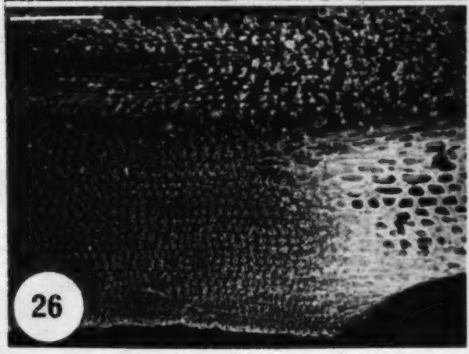
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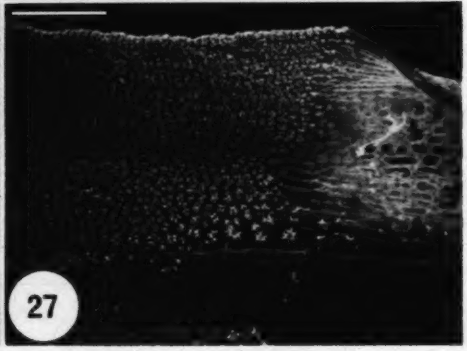
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considerably farther basipetally on the abaxial surface (Figs. 24-25). In others, the papillae extend almost as far down on the adaxial as they do on the abaxial surface (Figs. 26-27). When the papillae on the abaxial surface or on both surfaces extend down to the basal cells that are differentiated by colored walls, the impression is of a very abrupt transition from the upper cells to the basal cells . In contrast, when the transitional cell walls are smooth well above the basal cells with colored walls, the appearance is of a very gradual transition . Plants of Bryobrittonia have transitional cell walls that are smooth and bulging to plane basipetally on both surfaces.

The basal laminal cells are mostly oblong in shape (Figs. 28-31), but are generally both longer and wider than the transitional cells. The superficial walls are virtually smooth and plane in transverse section in Bryobrittonia and all species of Encalypta (Fig. 28), except E. affinis. In the latter species, there are papillae on the abaxial surface of the basal cells, particularly along the leaf margins (Figs. 30-31). The basal laminal cell walls are either hyaline in Bryobrittonia or they are brownish. Neither the transverse nor the longitudinal walls are thickened, or only slightly and evenly so. In contrast, in all species of Encalypta, the transverse walls are more-or-less thickened, particularly at the corners, and the longitudinal walls are thin. However, it is not so much the thickenings but the coloration of these walls that differentiates more-or-less the basal laminal cells in species of Encalypta. The transverse walls are more-or-less colored, at least in those cells nearer to the costa and the longitudinal walls are either hyaline or more-or-less colored. The pattern of coloration of the transverse and longitudinal walls, that is, shade of color and whether one or both are colored, is an important taxonomic feature that varies interspecifically in many instances. In some species, both the longitudinal and transverse walls are dark-orange, in others only the transverse walls are, while in still others the transverse walls are a very pale yellow.

A notable feature of the basal laminal cells of species of Encalyptaceae is the perforation of the walls (Fig. 29). As early as 1890 Limpricht reported that "...die glatten, dünnen Aussenwände zum Theil resorbirt, Querwänd verdickt und meist in der Mitte durchbrochen,...". Recently, Edwards (1979) reported that resorption pores occur in all three pottioid orders, that is, the Pottiales, Syrrhopodontales and Encalyptales. Furthermore, he pointed out that the shape and distribution of these pores is an

Figures 28-33. Basal Laminal Cells; Perigonia.

Figs. 28-31. Basal Cells of Species of Encalypta.

Fig. 28. Encalypta brevicolla. Abaxial surface showing basal cell walls entire. Scale=50 µm.

Fig. 29. Encalypta microstoma. Abaxial surface showing basal cell walls perforate. Scale=100 µm.

Figs. 30-31. Encalypta affinis. Abaxial surface showing papillose walls of basal cells.

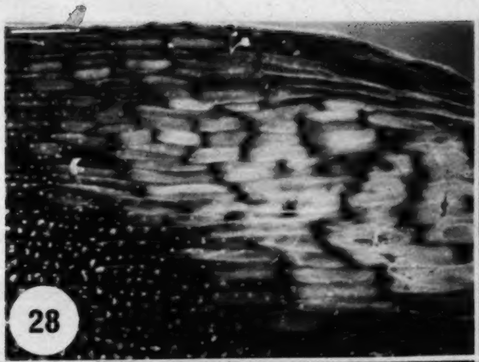
Fig. 30. Scale=100 µm.

Fig. 31. Scale=40 µm.

Figs. 32-33. Perigonia.

Fig. 32. Encalypta microstoma. Bud-like perigonium attached to base of costa. Scale=400 µm.

Fig. 33. Bryobrittonia longipes. Paraphyses with inflated upper cells and antheridia. Scale=200 µm.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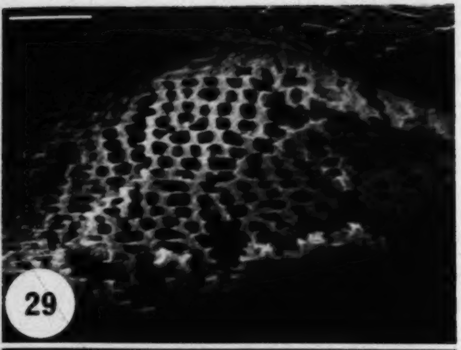
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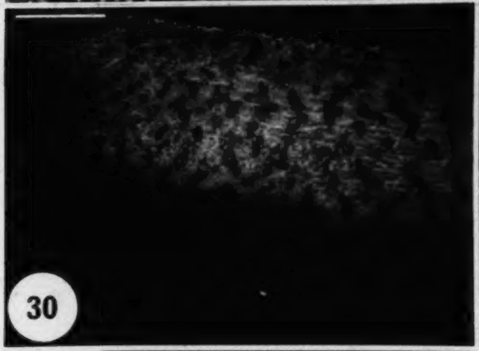
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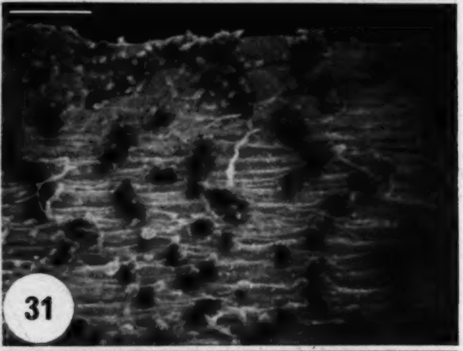
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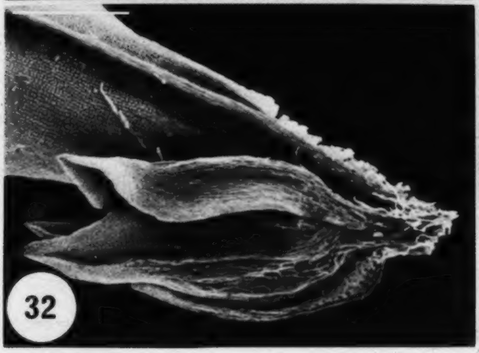
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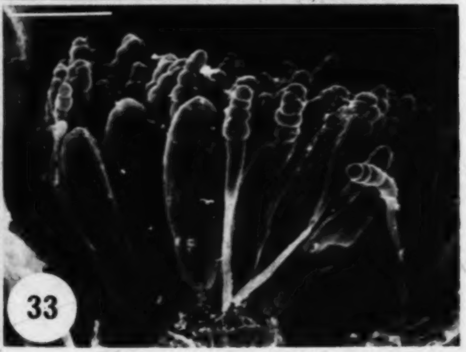
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important taxonomic feature at the family, subgenus, section and species level in the Calymperaceae. Nowak (1980) reported the occurrence of, and illustrated with SEM's, pores in the basal cells of species of Mitthyridium. In species of Encalypta the transverse walls are porose, each with a single large pore, while they are irregularly perforated in Bryobrittonia. The superficial cell walls on both the adaxial and abaxial surfaces are entire (Fig. 28) or irregularly more-or-less perforated (Fig. 29). in all species of Encalypta, but they are entire in Bryobrittonia. I have been unable to determine any specific differences in either the shape or distribution of the pores or perforations among the species of Encalypta in contrast to Edwards (1979), who was able to demonstrate such differences among the species of Calymperes that occur in western Africa.

In all species of Encalyptaceae the basal cells are more-or-less differentiated in shape marginally. That is, they grade from the broad, oblong laminal cells into narrower and short- to very long-oblong cells. Furthermore, in species of Encalypta there is a gradation from the basal laminal cells with strongly thickened transverse and thin longitudinal walls to marginal cells with slightly thicker longitudinal walls and less thickened transverse walls. As with the basal laminal cells, coloration is the most important taxonomic feature of the basal marginal cells. Some species of Encalypta have the basal marginal cells colored more-or-less as the basal laminal cells so that the former appear undifferentiated from the latter. In other species, there is a distinct, more-or-less broad, marginal border of cells that are uniformly pale green in color in contrast to the more-or-less colored walls of the basal laminal cells. In some taxa this marginal border includes cells that structurally would be considered basal laminal cells (that is, the transverse walls are strongly thickened). The presence or absence of this differentiated basal marginal border is a sound taxonomic criterion that is useful in distinguishing between many species of Encalypta. In the genus Bryobrittonia, the basal marginal cells are undifferentiated in color from the basal laminal cells. In a few species of Encalypta the upper corner of each cell in the outermost row of basal marginal cells is free so that the margins are minutely crenulate, but there is interspecific variation and the margins are entire in some populations. There are from two or three up to 20 rows of marginal cells, which grade into the basal cells towards the costa and basipetally. The gradation is very gradual in some species with indistinctly defined, that is, pale colored, basal cells and more abrupt in those with the basal cells dark colored. The walls of the marginal cells are generally smooth except in a few species of Encalypta which have papillae on the outer walls of the marginal cells.

Sexual Condition. Both the goniautoicous and the dioicous sexual conditions occur in the Encalyptaceae. Sporophytes are consistently found on plants in most populations of most species of Encalypta. Only in E. procera and E. streptocarpa are sterile populations of frequent occurrence, and E. streptocarpa is the only species of Encalypta that is dioicous. All other species are goniautoicous with lateral, bud-like perigonia borne below the terminal perichaetium along the stem or attached to the lower abaxial surface of a costa on a very short stalk (Fig. 32). The vegetative leaves grade into the perichaetial leaves, which are not much differentiated except for a more-or-less broad and relatively long, sheathing base. Also, the basal cells tend to be less distinctly differentiated with the transverse walls paler in color and less thickened than in the vegetative leaves. Generally, the perigonial leaves are very short, approximately one millimetre long, and broadly sheathing. The shape of the leaf apex tends to correlate with that of the vegetative leaves. In other respects, cell shape and size, ornamentation and coloration of the walls, the perigonial leaves are more-or-less like the vegetative leaves, allowing that some of the features are necessarily obscured by the reduction in size. There are approximately five or six antheridia surrounded by numerous paraphyses, but the number is somewhat variable.

Encalypta streptocarpa and Bryobrittonia are the two species of Encalyptaceae that are dioicous. Few populations of Bryobrittonia have been found with sporophytes, yet there are many collections of E. streptocarpa with sporophytes. Concerning E. streptocarpa, Limpricht (1890) observed "...in der Ebene selten und meist steril, häufig durch das gesammte Bergland, hier an beschatteten Stellen oft reichlich fructend, in höheren Lagen des Alpengebietes fast nur steril.". In both Bryobrittonia and E. streptocarpa, even in those populations with sporophytes, perigonia are rare and the number of plants with sporophytes greatly outnumber those with perigonia. In populations of Bryobrittonia that consist of plants without sporophytes, archegonia are generally present, but antheridial plants do not occur. I have seen the opposite situation, of a population consisting solely of antheridial and sterile plants, only once. The terminal perigonia are relatively massive and, with the surrounding leaves, appear not unlike the inflorescence of some Compositae. The perigonial leaves are little differentiated from the vegetative leaves, except that they tend to be somewhat broader and sheathing, and shorter. The number of antheridia probably approaches thirty or forty and these are surrounded by a mass of paraphyses.

As noted above, Saito (1975) reported paraphyses, in contrast to axillary hairs, to be uniformly thick-walled and pale yellowish-brown. In all species of Encalyptaceae they are hyaline with only the upper walls slightly thickened. Species of Encalypta have the walls uniformly smooth on all paraphyses or there are some with very sparse, low, rounded papillae. While I have not found the latter feature in all species of Encalypta, I suspect that it is a sporadic variation that probably occurs in most, if not all. These papillae have not been observed in Bryobrittonia. Another modification is that the upper cells of some paraphyses are divided longitudinally. This characteristic occurs in Bryobrittonia and has been observed in some species of Encalypta, but as with the papillae, probably occurs in most. Among the species of Encalypta, the cells of the paraphyses are more-or-less uniform in size. In contrast, those of Bryobrittonia are differentiated with the lower cells of comparable size to all of the cells in Encalypta, but the upper cells in Bryobrittonia are quite abruptly enlarged (Fig. 33).

Seta: In the Encalyptaceae, the length and color of the seta are important taxonomic features. While there is some intraspecific variation in length, the interspecific differences are generally greater. The seta is as short as one or two millimetres in some species and as long as 30 millimetres in others. In most species of Encalyptaceae the color tends to be constant within a species and varies from yellow, orange or red to almost black. In some species the seta is a different color near the base of the capsule. When the seta is old, it is dull-orange in most species and therefore not taxonomically useful. The seta is slightly twisted sinistrorsely in the lower part, except in those species with a very short seta, and more-or-less strongly twisted dextrorsely just below the capsule. There is little interspecific variation in the diameter of the seta, and in most species the diameter is much the same throughout the length of the seta. However, in

Bryobrittonia and E. streptocarpa the seta is generally more-or-less tapered distally so that it is smaller in diameter near the base of the capsule than it is where it connects with the vegetative plants. In transverse section, the structure of the seta is virtually identical throughout the Encalyptaceae (Fig. 34). There is a distinct central strand of minute, parenchymatous cells with thin, yellowish walls. Such cells have been considered to be hydroids (Hébant 1977). Surrounding the central strand are more-or-less enlarged cells with thick, orange walls. The cells are progressively smaller and the walls thicker centrifugally. The significance of such anatomical structure has been reviewed by Hébant (1977).

Capsule: In all species of Encalyptaceae, the erect capsule is cylindric (Figs. 40-46); however, there are specific distinctions in finer aspects of the shape. For example, the capsule is perfectly smooth with a turgid appearance in some species (Figs. 40, 44), delicately striate (Figs. 41, 42)or distinctly plicate (Figs. 43, 45)in others. Also, in most species, there is a more-or-less distinct constriction just below the mouth of the capsule (Figs. 40-41, 43, 45-46), while some have the capsule contracted to the mouth (Fig. 44). In most species of Encalyptaceae the capsule consists only of an urn, but a short neck is distinctly differentiated in E. longicolla (Fig. 46) and indistinctly in some populations of E. affinis and E. brevicolla. In several species of Encalypta there occur capsules that are more-or-less markedly different in shape from those characteristic for that species. The most notable features of extreme forms of such capsules are the minute mouth (Fig. 239) and, in those species with a peristome, the distorted teeth. In some, the operculum is indehiscent. There is structural intergradation between these capsules, which I term aberrant, and those that are typical for a species. Also, plants with aberrant capsules are differentiated in no other features and, as noted above, the occurrence of aberrant capsules traverses interspecific boundaries. Therefore, aberrant capsules are regarded as some kind of a developmental abnormality and are given no formal taxonomic recognition. For further discussion of aberrant capsules, see Diagnosis and Differentiation of E. microstoma.

Color of the capsule is an important taxonomic feature and the interspecific variation is greater than the intraspecific. In some species, capsules are distinctly yellow

Figures 34-39. Anatomy of Seta; Structure of Capsule.

Fig. 34. *Bryobrittonia longipes*. Transverse section of seta. Scale=50 µm.

Fig. 35. *Encalypta streptocarpa*. Revoluble annulus. Scale=40 µm.

Figs. 36-37. Transverse sections showing variation in thickening of exothecial cells.

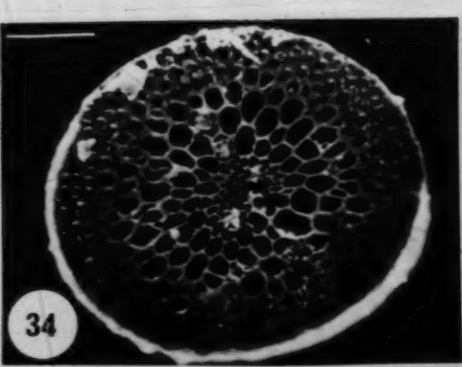
Fig. 36. *Encalypta microstoma*. Note thickening of both superficial and radial-longitudinal walls. Scale=40 µm.

Fig. 37. *Encalypta brevicolla*. Note slight thickening of superficial walls. Scale=20 µm.

Figs. 38-39. Phaneroporous stomata.

Fig. 38. *Encalypta streptocarpa*. Stomata restricted to base of capsule. Scale=100 µm.

Fig. 39. *Encalypta ciliata*. Scale=20 µm.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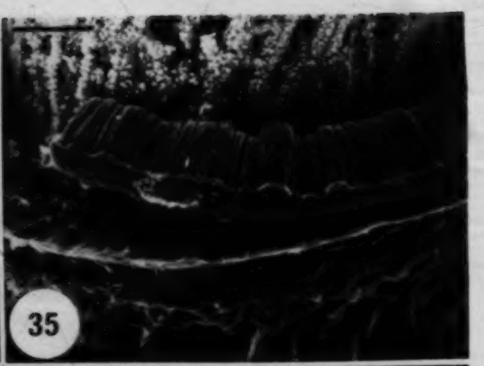
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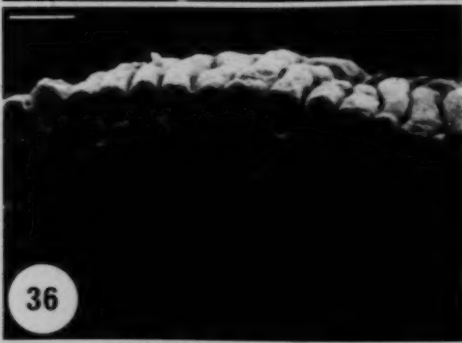
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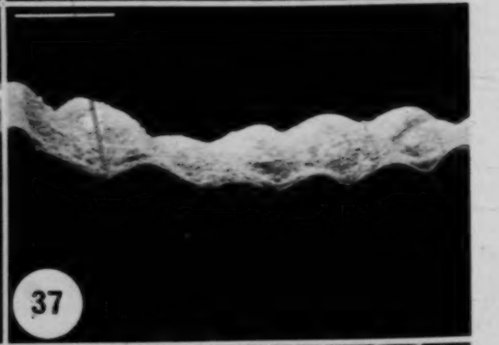
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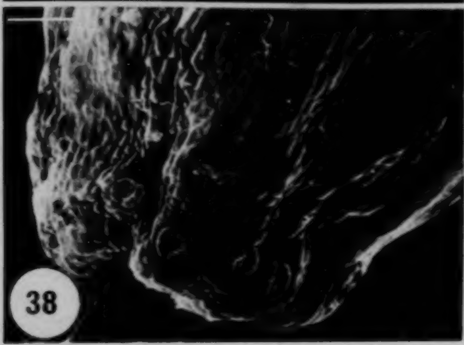
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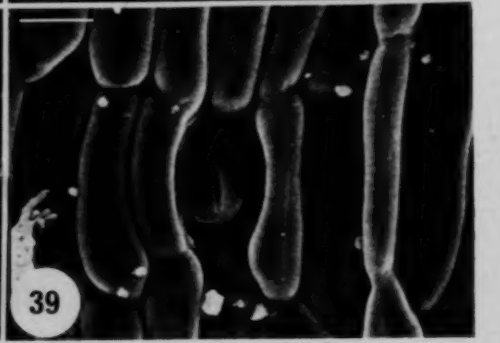
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Figures 40-46. Variation in Capsule Shape. Scale=1 mm.

Fig. 40. Encalypta ciliata.

Fig. 41. Encalypta brevicolla.

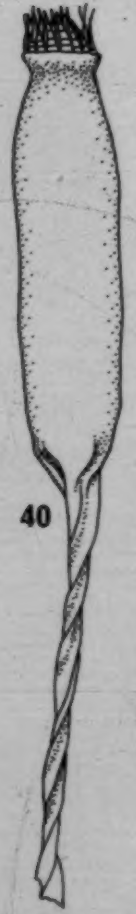
Fig. 42. Encalypta mutica.

Fig. 43. Encalypta vittiana.

Fig. 44. Encalypta microstoma.

Fig. 45. Bryobrittonia longipes.

Fig. 46. Encalypta longicolla.



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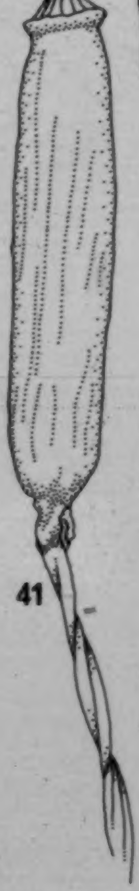

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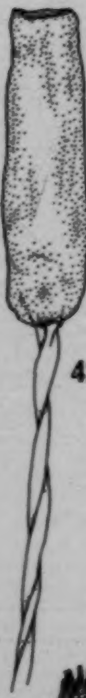

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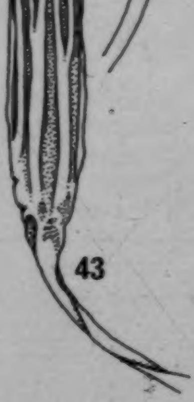

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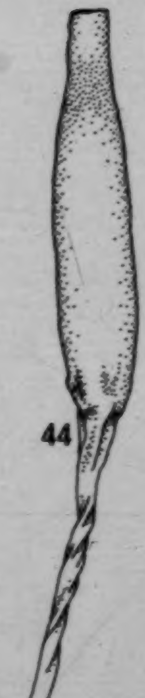

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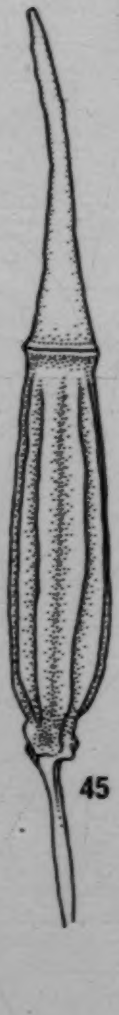

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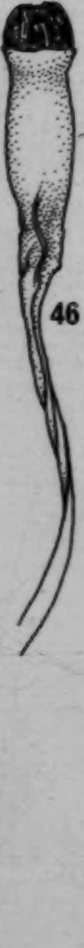

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or dark-orange, while the tones are much less vibrant in others that are pale-golden or pale-brown. Generally, there is a more-or-less bright-red rim at the mouth of the capsule. The width of this rim, as well as the shade of red are important for making distinctions at the specific level.

Exothecial Cells: The exothecial cells are rather irregularly oblong with square corners, and they are quite broad and short (1:2) or longer and narrower (1:8). The superficial walls are smooth. In most species of Encalyptaceae, the exothecial cells are arranged in more-or-less regular, longitudinal rows, but in a few the rows are spiral. At the base of the capsule and just below the rim, the exothecial cells are markedly shorter and the walls are thicker. I have been unable to find any taxonomically significant variation in the shape of the exothecial cells; however, the thickness of the walls and the location of the thickenings are important. In transverse section through the mid-portion of the capsule, the superficial and adjoining radial-longitudinal walls are thin in some species, in others only the superficial walls are more-or-less thickened (Fig. 37). These thickenings are restricted to groups of cells with other groups of thin-walled cells in between or, in other instances, the thickenings are continuous. There are a few species of Encalypta in which the superficial and adjoining radial-longitudinal walls are strongly thickened in such a manner that they give the appearance of a cut-out paper chain of tulips (Fig. 36).

Rim Cells: In all species of Encalyptaceae, one to eight rows of cells are more-or-less differentiated at the mouth of the capsule. The variation is primarily interspecific. In some species there are only one or two rows, while in others there are six or eight. The rim cells are generally quadrate (1:1) to subquadrate (0.5:1) or short-oblong (1:2) and the walls are thin to quite strongly thickened. In a few species the upper ends of cells in a lower row slightly overlap the cells in the next row above.

Stomata: Phaneroporous stomata (Figs. 38-39) characterize all but two species of Encalyptaceae. In these two, Bryobrittonia and E. streptocarpa, the stomata are either phaneroporous or slightly cryptoporous. The stomata, which are oriented parallel with the long axis of the capsule, are composed of two guard cells with subsidiary cells undifferentiated (Fig. 39). Paton and Pearce (1957) reported them to be of the long-pore type. There is some interspecific, as well as intraspecific, variation in guard cell size, particularly in length, and in many instances, the guard cells that form a single stoma are of different lengths. The guard cells are 25 to 50 microns long in some species, 30 to 60 in others and as much as 50 to 70 microns in one. The stomatal apparatus is generally 20 to 40 microns in width. The position and number of stomata on the capsule are important taxonomic features. They occur randomly over the surface of the capsule in some species, but in others they are restricted to the base of the capsule. Density of stomata varies independently of position; however, Paton and Pearce (1957) reported that in many mosses there is a general relationship between length of the seta and number of stomata. They reported 50 stomata in *E. streptocarpa*, 30 in *E. ciliata* and 15 in *E. rhaptocarpa*.

Peristome: There is considerable variation in the structure of the peristome in the Encalyptaceae. An outline of this variation follows with a more extensive discussion, based on Philibert's (1889) work and my own observations, in the section on phylogeny. Some species are characterized by a peristome that consists of two, more-or-less fused layers with sixteen outer teeth positioned opposite sixteen inner segments (Fig. 47). The outer teeth (exostome) are long and linear with a vertical line extended along the middle of each tooth on the outer surface (Fig. 54). In some, the teeth are more-or-less joined basally by a very low, fenestrate membrane. There are more-or-less well-developed trabeculae on the inner surface of each exostome tooth (Figs. 53,55). The inner segments (endostome) arise from a well-developed, pleated basal membrane (Figs. 56-57) and are shorter than the outer teeth. On the outer surface of the basal membrane, the joint between each segment consists of two, fused, revolute flanges (Fig. 56). These joints are positioned alternate to the outer teeth. The outer surface of each endostome segment is undivided (Fig. 56). On the inner surface, near the base of the basal membrane, each segment consists of two cell plates (Figs. 55,57). Both the teeth and segments are more-or-less roughened or ornamented by irregular, granular papillae.

Other species have a single row of sixteen teeth. In some, these are linear and consist of two almost completely fused, opposite layers (Figs. 48-49, 58-60). The teeth

Figures 47-52. Peristome Types in the Encalyptaceae.

Fig. 47. *Encalypta procera*. Double peristome with two rows of more-or-less unfused, opposite teeth. Scale=200 μm.

Figs. 48-49. Double peristome with two rows of fused, opposite teeth. Scale=100 μm.

Fig. 48. *Encalypta longicolla*.

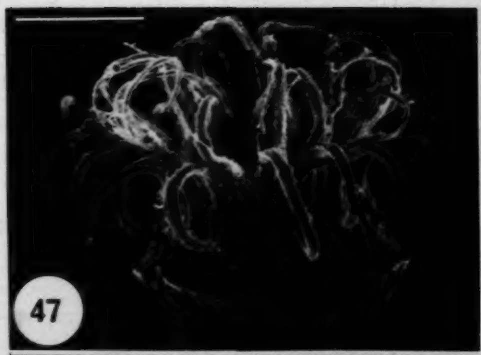
Fig. 49. *Encalypta brevicolla*.

Figs. 50-51. *Encalypta ciliata*. Single peristome. Scale=100 μm.

Fig. 50. Teeth well-developed.

Fig. 51. Peristome vestigial; teeth fragile.

Fig. 52. *Encalypta brevipes*. Peristome absent. Scale=200 μm.



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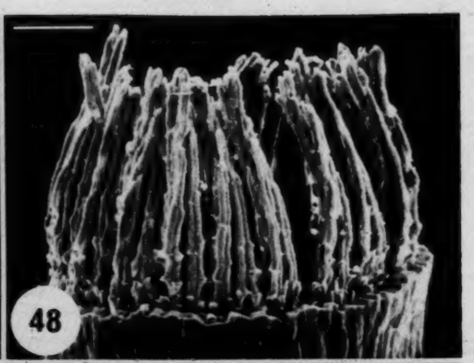

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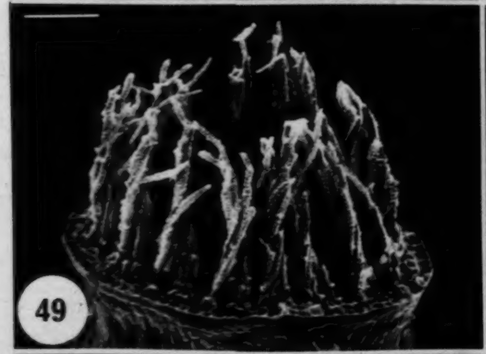

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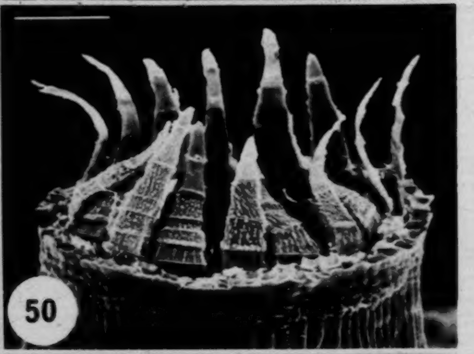

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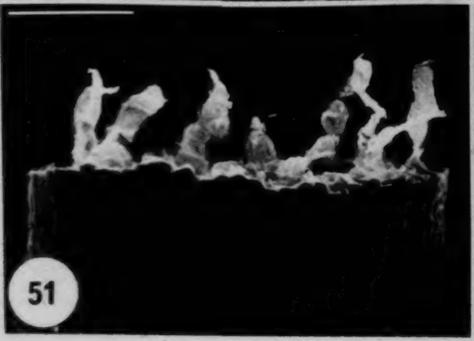

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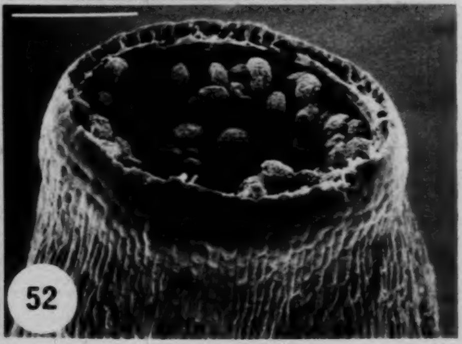

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Figures 53-56. Details of Peristome Structure. Scale=40 µm.

Figs. 53-54. Encalypta streptocarpa. Exostome.

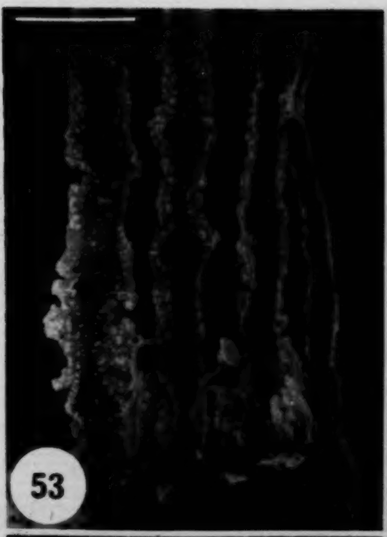
Fig. 53. Inner surface. Note trabeculae.

Fig. 54. Outer surface. Note vertical division of each tooth.

Figs. 55-56. Bryobrittonia longipes.

Fig. 55. Inner surface of endostome and exostome (right). Note vertical division of endostome and trabeculae of exostome.

Fig. 56. Outer surface of endostome. Note that each segment is undivided.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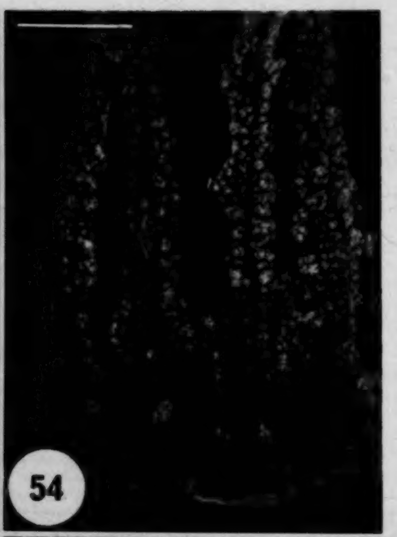
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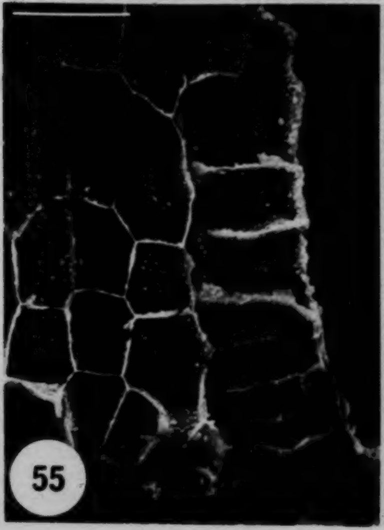
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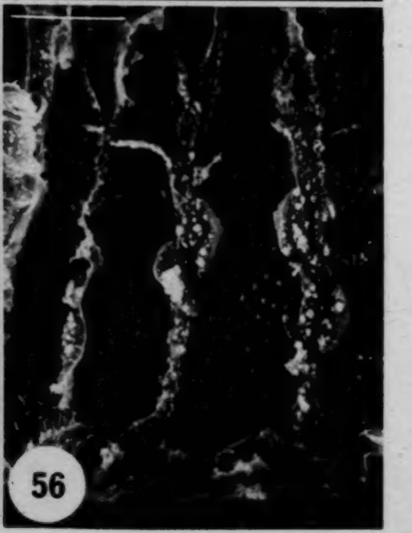
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Figures 57-60. Details of Peristome Structure (cont'd).

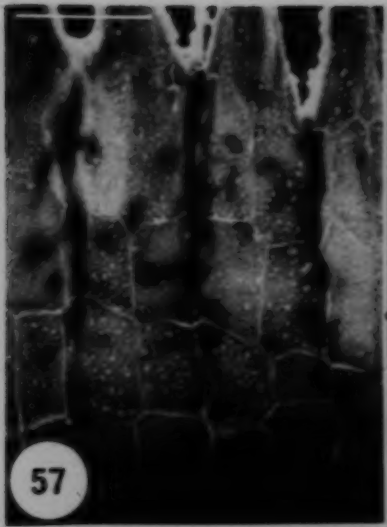
Fig. 57. *Bryobrittonia longipes*. Endostome, inner surface. Note that each segment is vertically divided into two. Scale=50 μm.

Figs. 58-59. Outer surface of fused, double peristome showing vertical division of each tooth, and exostome and endostome.

Fig. 58. *Encalypta longicolla*. Scale=100 μm.

Fig. 59. *Encalypta brevicolla*. Scale=50 μm.

Fig. 60. *Encalypta brevicolla*. Inner surface of fused, double peristome with vertical division of each tooth. Scale=40 μm.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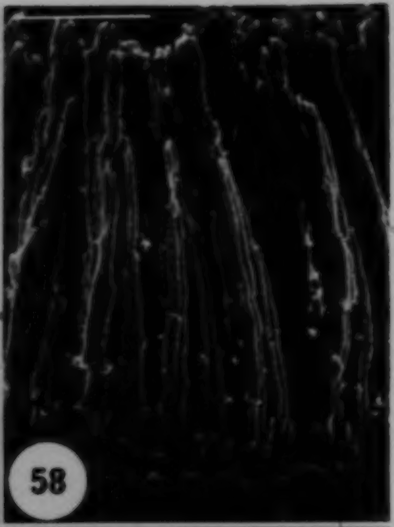
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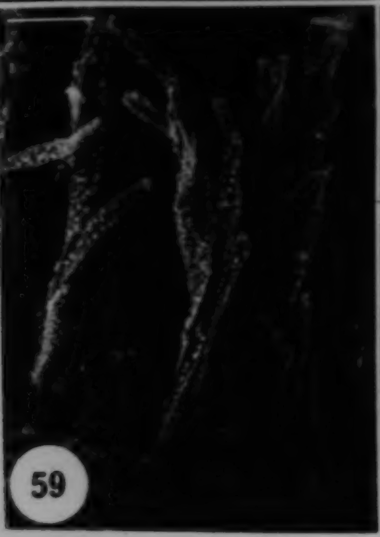
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in this type of peristome appear somewhat irregular as if each is composed of linear bundles of cells; however, the structure of the outer and inner surfaces is more-or-less similar to that of the outer surface of the exostome and the inner surface of the endostome, as described above, except that there is no basal membrane (Figs. 58-60). Another type of single peristome is that which I term the ciliata-type. Such a peristome consists of a single layer of sixteen, lanceolate teeth (Fig. 50), although a partial secondary layer, or preperistome (Fig. 63), is present in some populations. There is no vertical division on the outer surface of each tooth (Fig. 61), but the preperistome is vertically divided (Fig. 63). The structure of the inner surface is with two cell plates basally (Fig. 62), as described above. The outer surface is more-or-less ornamented, but the inner is smooth (Figs. 61-62).

Development of the ciliata-type peristome is variable both within and between species. Relative development is most readily determined by the color of the teeth. These are dark-orange in well-developed peristomes and pale orange or hyaline in those that are poorly developed. When the peristome is very poorly developed, the teeth are more-or-less truncate and the papillae are sparse (Figs. 51,64). I term such hyaline, poorly developed peristomes vestigial. A number of species of Encalypta are characterized by the lack of a peristome (Fig. 52). However, rare populations of some species that generally have gymnostomous capsules have a vestigial peristome.

Saito (1975) described the origin and nature of the hymenium that occurs in some species of Pottiaceae as follows: "The cells of the upper portion of [the] columella in the eperistomate capsule...are also shrunken when mature and mostly break off with [the] operculum, but the marginal cells of the columella sometimes remain at the mouth of the capsule and later constitute the hymenium in some species...". Among the gymnostomous species of Encalypta, there is a noticeable ring of tissue inside the rim of the capsule in only one, E. alpina (Figs. 122-123). This tissue may represent a hymenium as described by Saito.

Operculum: Variation in the shape of the operculum more-or-less parallels that of the peristome. Those species with a double peristome have an operculum that is long and narrowly conic-rostrate; at the other extreme are those species that have a single,

Figures 61-64. Details of Peristome Structure (cont'd.).

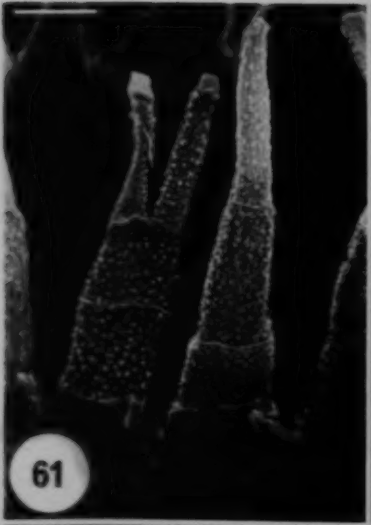
Figs. 61–62. Encalypta ciliata. Scale=40 μm.

Fig. 61. Outer surface of tooth. Note papillae.

Fig. 62. Inner surface of tooth. Note vertical division of each tooth in lower part.

Fig. 63. Encalypta rhaptocarpa. Preperistome. Note vertical division. Scale=10 μm.

Fig. 64. Encalypta ciliata. Outer surface of tooth of vestigial peristome. Note lack of papillae marginally. Scale=40 μm.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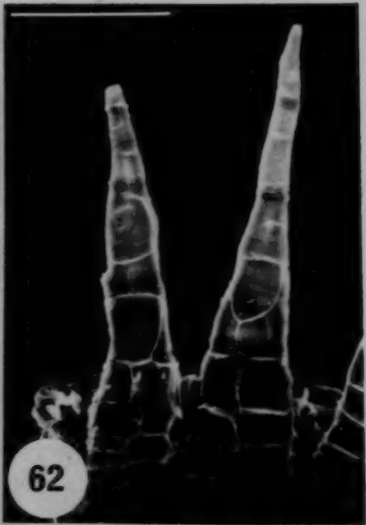
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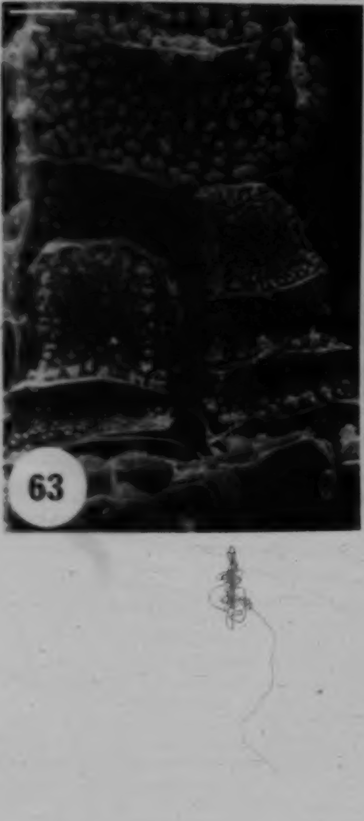
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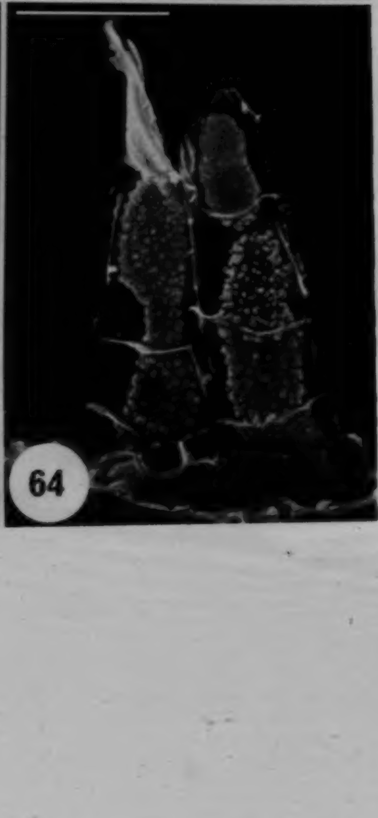
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ciliata-type peristome or those that lack a peristome and these are characterized by an operculum that is more-or-less plane-convex and long- or short-rostrate. Two to three rows of cells at the base of the operculum are more-or-less differentiated. In size, shape and color, they are similar to the rim cells of the capsule.

Annulus: Most species of Encalyptaceae do not have a differentiated annulus, but in Bryobrittonia, E. streptocarpa and E. procera there occurs a well-developed, more-or-less deciduous annulus (Fig.)that consists of two or three rows of cells. In surface view, the cells are bright-red and glossy, but small and quadrate. However, in lateral view they are considerably enlarged inwardly, and the walls are hyaline and appear inflated.

Spores: There is considerable variation not only in size, but also in the structure and sculpture of spores of Encalyptaceae, particularly between species, as the studies of Vitt and Hamilton (1974) and Járai-Komlódi and Orbán (1975) illustrate. The spores are unicellular and never germinate precociously; however, they do germinate readily in/on a nutrient-free medium or substrate. They range in size from seven to 80 microns and are either green, orange or brown. In general, intraspecific variation in spore size is 10 to 15 microns or less, while intrapopulational variation is very slight, perhaps one to three microns. Also, color of spores varies interspecifically, not intraspecifically, in most instances. However, in Bryobrittonia, exceptional intrapopulational variation in both size and color have been recorded, as well as other irregularities in spore structure (see discussion of Variation under B. longipes). It also appears that in some populations of E. streptocarpa there is exceptional variation in size of spores. The spores of most species of Encalyptaceae appear to be atreme, that is, without a distinct aperture, but Erdtman (1965) suggested that several such species might be katalept, a condition that he described as "...provided with a thin, more or less trema-like area [=aperture] in the proximal face.". One species, E. ciliata, has a very distinct trilete aperture on the proximal face (Fig. 69) and a few others are characterized by a more-or-less distinct trilete mark. In some species the spores are circular to elliptical and isopolar with the structure and scrulpturing of the exospore more-or-less uniform over the entire surface (Fig. 65).

Figures 65-70. Spore Types in the Encalyptaceae.

Fig. 65. Bryobrittonia longipes. Isopolar, minutely gemmate. Scale=4 μm.

Figs. 66-67. Encalypta affinis. Paraisopolar, gemmate. Scale=10 μm.

Fig. 66. Distal face.

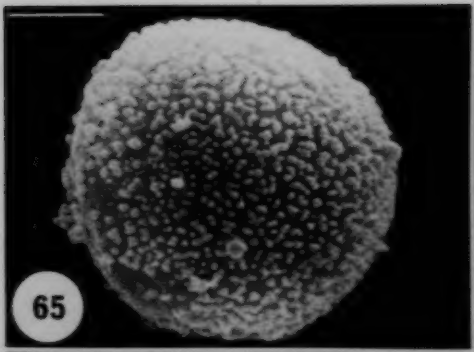
Fig. 67. Proximal face.

Figs. 68-69. Encalypta ciliata. Heteropolar. Scale=10 μm.

Fig. 68. Distal face. Note central pit surrounded by rim and radiating ridges.

Fig. 69. Proximal face. Note triradiate mark.

Fig. 70. Encalypta flowersiana. Distal face showing verrucate and vermiform protuberances. Scale=10 μm.



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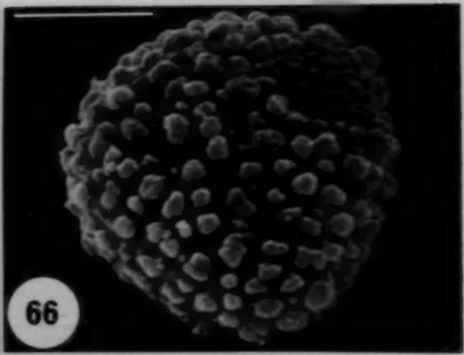

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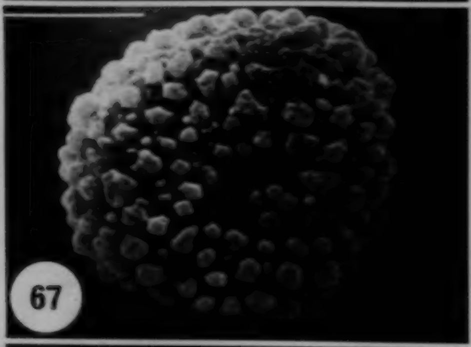

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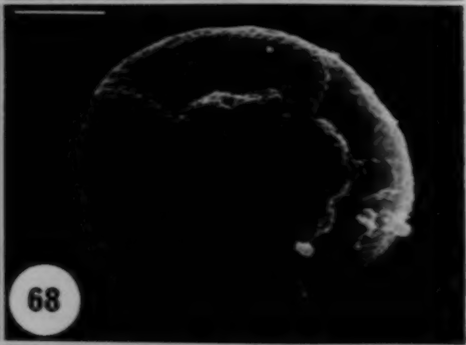

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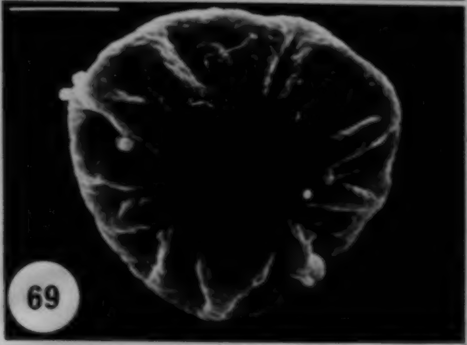

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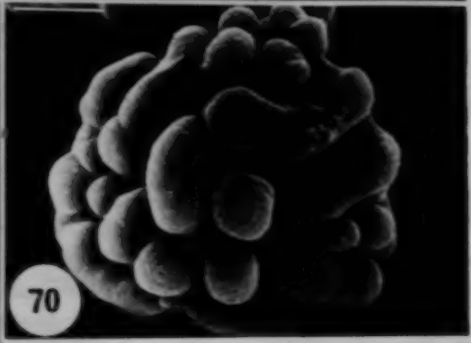

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Other species, in contrast, have heteropolar spores. These are circular in polar view, but more-or-less concave- or plane-convex in lateral view, and both the structure and sculpture are quite different on the proximal and distal faces (Figs. 66-67). A third group of species is characterized by paraisopolar spores that exhibit some weak differentiation in shape and, in some instances, in structure and/or sculpturing of the two faces (Figs. 68-69). All species of Encalyptaceae have intectate spores, but several different structural types occur including scabrate (Fig. 65), gemmate (Figs. 66-67), verrucate and vermiform (Fig. 70). The size of these structures varies from one or two microns in diameter to eight, and in one species the vermiculate processes are up to 40 microns in length. In a number of species there are also small to medium sized granules, possibly a perine deposition, in specific areas or randomly scattered over the surface. Sculpturing types include rugulate, striate and reticulate patterns. Erdtman (1965) described, in palynological terms, the spores of _E. affinis_, _E. alpina_, _E. ciliata_, _E. rhaptocarpa_ and _E. streptocarpa_, and figured three of these (Erdtman 1957). In the context of a survey of the different spore-types that occur in the Musci, McClymont (1954) described and figured the spores of _E. ciliata_, _E. procera_ and _E. rhaptocarpa_. A discussion of the evolutionary significance of the different spore-types that occur in the Encalyptaceae is included in the section on Phylogeny.

Calyptra: The calyptra is an inconspicuous structure that does not remain associated with the plants for long in most groups of mosses; however, in the Encalyptaceae it is remarkably amplified in many instances and persists in association with the sporophyte long after the spores have been dispersed. All species of Encalyptaceae are characterized by a mitrate, cylindric-campanulate calyptra that is naked and non-plicate (Figs. 71-79). It extends at least to the base of the capsule, but in many the calyptra is considerably longer than the capsule. There are taxonomically useful, interspecific differences in a number of features of the calyptra, including shape, size and color.

The calyptra can be subdivided into three parts, the rostrum, the cylinder and the fringe (Fig. 74), but the latter is not present in all taxa. The definition of the rostrum is an important characteristic and is, in general, a reliable basis for distinguishing between species. In some species the cylinder is narrowly cylindric and tapered distally to an

Figures 71-79. Variation in Structure of Calyptra. Scale=1 mm.

Fig. 71. _Encalypta streptocarpa._

Fig. 72. _Encalypta mutica._

Fig. 73. _Encalypta brevicolla._

Fig. 74. _Encalypta ciliata._

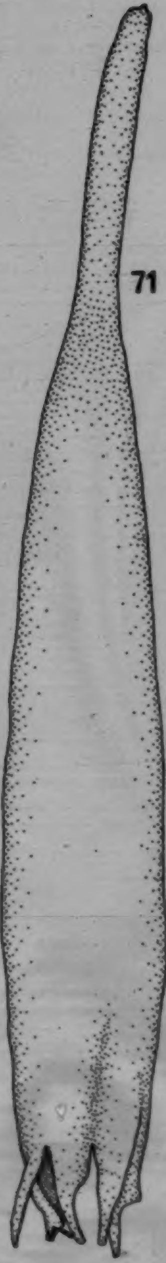
Fig. 75. _Encalypta asperifolia._

Fig. 76. _Encalypta brevipes._

Fig. 77. _Encalypta procera._

Fig. 78. _Encalypta intermedia._

Fig. 79. _Encalypta alpina._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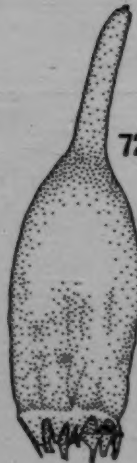
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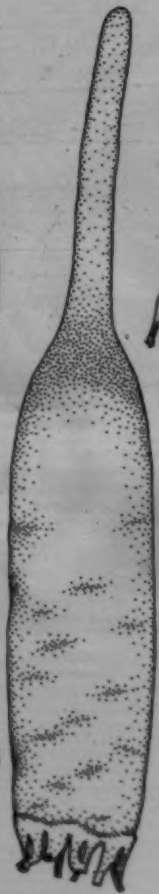
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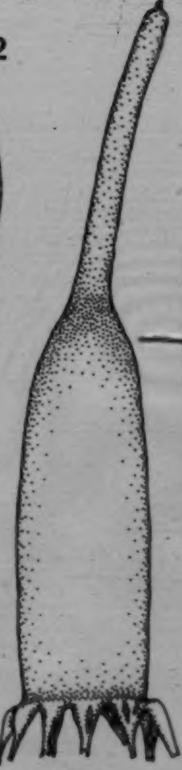
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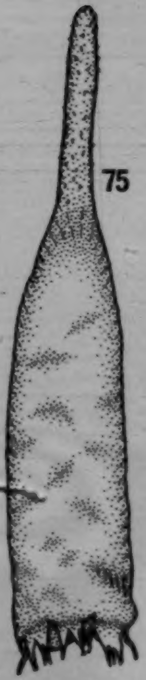
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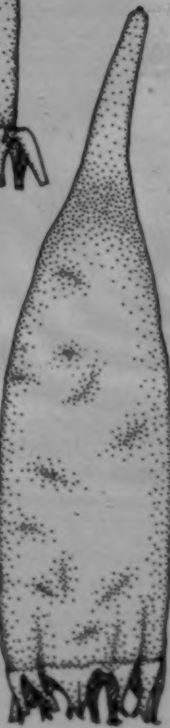
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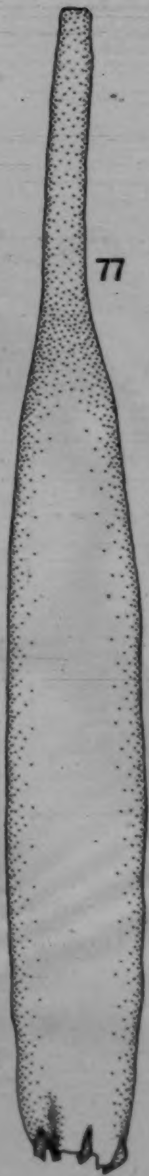
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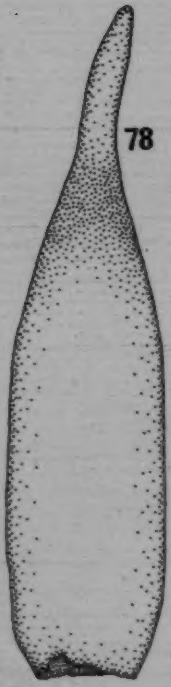
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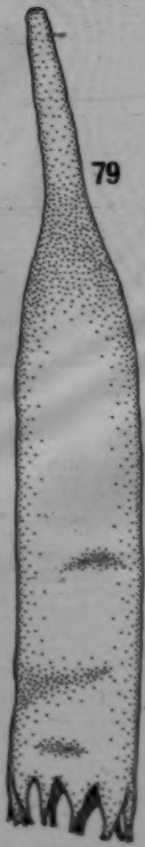
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ill-defined rostrum (Figs. 71, 77). In others the cylinder is broader and the transition to the rostrum is less gradual (Fig. 79) or even abrupt (Figs. 73-74) so that the rostrum is very clearly differentiated from the cylinder. The base of the cylinder is entire in some taxa (Fig. 78), but in most it is either lacerate (Fig. 71) or fringed (Figs. 72-76). When the cylinder is lacerate it consists of four or six broad segments that are an extension of the cylinder. With age these segments generally are broken off leaving a more-or-less erose base (Fig. 77). In other species, there is a more-or-less distinct constriction or contraction at the base of the cylinder above narrower and mostly shorter fringe-like segments (Figs. 72-73, 75-76). The ultimate development of the fringe occurs when the base of the cylinder is narrowly extended horizontally and the fringe hangs pendent from this extension (Fig. 74). Even when the fringe segments are broken off, as they generally are in older calyptrae, the basal extension remains. In those species with a lacerate base, the segments generally consist of several layers of cells in transverse section. In contrast, the fringe, particularly in those species where it is well-developed, consists of a single layer of cells with markedly thickened walls. The calyptra is unornamented in some species, but in many at least the rostrum is more-or-less papillose or scindulose (Fig. 75). Fewer taxa have the papillae and/or scindulae on the cylinder as well and they occur on the fringe in only one species. The cylinder is smooth in some species, but more-or-less puckered in others. There is also some intraspecific variation in this characteristic.

The total length of the calyptra is subject to considerable interspecific variation. It is as much as ten millimetres (Figs. 71, 77) in some species and as little as two in others (Fig. 72). The rostrum is similarly variable in length with some that are relatively long (two millimetres) (Figs. 73-74) and others that are considerably shorter (just less than one millimetre) (Fig. 72, 76, 78). Length of the rostrum does not necessarily correlate with length of the cylinder and the relative proportions of these are important in differentiating between some taxa.

Some species of Encalyptaceae are characterized by a calyptra that is dark golden-brown and opaque so that the capsule is not visible through it. At the opposite extreme are those species with the calyptra pale golden and transluscent so that even some structural details of the capsule are apparent. These interspecific differences in the color of the calyptra can be loosely correlated with the number of layers of thick-walled cells that comprise the cylinder. In transverse section the cylinder is composed of from two to five layers of very thick-walled cells with small lumina to the outside and one or two inner layers with enlarged lumina and thin walls. The latter are generally partially collapsed.

On the basis of an analysis of the different calyptra-types that occur in the Musci, Janzen (1917) considered the structure of the encalyptaceous calyptra most similar to that of *Timmia* and *Atrichum* (as *Catharinaea*)-*Oligotrichum*-*Polytrichum*. As noted in the discussion of earlier treatments of the Encalyptaceae, Fleischer (1904) suggested that the calyptra of species of *Encalypta* is such a unique feature that it warrants separating these species in classifications. The evolutionary significance of the calyptra is dealt with in the section on Phylogeny.

Cytology: Chromosome numbers of n=12, 13, 14, 26, 27, 39 and 52 have been reported in the Encalyptaceae (Table 3). Among these numbers, n=13 is the most prevalent and n=26 is of frequent occurrence. *Bryobrittonia longipes* and *E. vulgaris* are the only species presently known with more than one chromosome number. *Bryobrittonia longipes* is also the only species reported with n=52 (as well as n=13, 26). Recently, Smith (1978) has suggested that the base number in the Haplolepideae is probably x=7. Therefore, on the basis of the presently available data, the species of Encalyptaceae are probably polyploid derivatives.

Most species of Encalyptaceae produce spear-stage sporophytes in the fall that expand the following spring. Limpricht (1890) reported species of *Encalypta* to have ripe spores between April and September, with some differences between individual species. In the course of my field studies, I have also observed specific differences in the ripening of sporophytes. For example, sporophytes of *E. rhaptocarpa* generally undergo meiosis earlier than those of *E. procera*; however, such differences are probab modified, to some extent, by variation in latitude and/or altitude as well as microhabitat differences. Anderson and Crum (1958), and others have described the general appearance of capsules when they are about to undergo meiosis. In the genus *Encalypta*, preliminary observations indicate that there are species-specific differences in the appearance of

Table 3. CHROMOSOME NUMBERS REPORTED IN THE ENCALYPTACEAE

Species	**Chromosome Number n=**	
Bryobrittonia longipes	52	(Lazarenko 1967)
[as *B. pellucida*]	13, 26	(Inoue 1974)
Encalypta affinis	13	(Anderson & Crum 1958)
	13	(Fig. 154)
E. alpina	14	(Steere 1954)
E. ciliata	13	(Anderson & Crum 1958)
	13	(Smith & Newton 1968)
E. longicolla	13	(Horton 1979a)
E. mutica	12	(Horton 1979a)
E. procera	27	(Steere 1954)
E. rhaptocarpa	26	(Steere 1954)
E. vulgaris	26	(Visotskaya 1967)
	26	(Smith & Newton 1968)
	39	Lazarenko *et al.* 1968)
var. *mutica*	13	(Steere *et al.* 1954)
	~~14~~	(Khanna 1967)

the capsules; however, I have found in most species that the spore mother cells have undergone meiosis once there is any suggestion of red color at the mouth of the capsule. Also, in those species with a peristome, the latter is well-developed at the time of meiosis.

In most species of Encalypta, the spore mother cells are reported to be approximately 50 microns in diameter (Anderson & Crum 1958, Horton 1979a, Smith & Newton 1968, Steere 1954, Steere et al. 1954). However, those of E. longicolla are approximately 90 to 100 microns (Horton 1979a), while those of E. affinis have been reported to be approximately 25 microns (Anderson & Crum 1958), although I have found them to be as large as 39 microns. Anderson and Crum (1958) suggested that perhaps the size of the spore mother cells of E. affinis bore some correlation with the actual spore size. Spores of E. affinis are relatively small (20 to 28 microns) compared to other species of Encalypta, and those of E. longicolla are the largest in the genus (55 to 75 microns). Therefore, it appears that there may be a general correlation between spore mother cell and spore size.

ENCALYPTACEAE Schimper,

Coroll. Bryol. Eur. 38. 1855 (1856).

Plants perennial, acrocarpous with terminal archegonia and subterminal innovations, to 50 mm tall, green to olive-green above, some with yellow, brown, black or glaucous overtones, brown to black below, ± branched or (in Bryobrittonia) unbranched. Stem in transverse section with epidermal cells in 1–3 rows, lumina small, walls ± thickened, orange to dark-orange, cortical cells parenchymatous, somewhat irregular in size, walls thin with slight corner thickenings, yellow to orange, dark-orange in few, central strand undifferentiated or indistinct in most, when present cells small to minute, walls very thin with corners very slightly thickened, hyaline to yellow, orange in few. Brood bodies absent in most, when present in ± dense clusters among leaves, filamentous, up to 3 mm long, upper part profusely branched, filaments discrete, dark-brown, lower part with up to 10 or 12 filaments joined laterally. Axillary hairs sparse or (in few taxa) abundant, filamentous, up to 2 mm long, joined laterally at base, covered by gelatinous substance. Leaves when dry sheathe slightly below, erect to erect-spread above with apices ± incurved, irregularly to (in few) regularly ± twisted, laminae inflexed to conduplicate or (in few) plane, involute or slightly reflexed, ±undulate in some; when moist erect-spread to reflexed, laminae inflexed to plane; 1.0–8.0 mm long, 0.2–2.0 mm wide, oblong to ligulate, lingulate, obovate-oblong, elliptic-oblong, ovate-oblong or ovate-lanceolate, apex ± abruptly or quickly narrowed to (in few) gradually narrowed, and muticous, mucronate, apiculate or hair-pointed; margins plane to recurved, entire or (in Bryobrittonia) crenulate in the upper half. Costa strong, ends well below apex to excurrent, abaxial surface ± prominently to (in few) inconspicuously keeled, shiny and smooth to ± dull and papillose, green, yellow, dark-brown or dark-red, adaxial surface smooth in lower third, papillose or (in Bryobrittonia) smooth with laminal-type cells above; in transverse section adaxial epidermal cells slightly smaller than laminal cells, 1–3 rows of ventral cells, lumina moderately large to large, walls strongly thickened, begleiters undifferentiated or (in few) well-developed in small central cluster below guide cells, lumina minute to small, walls thin, 2–8 rows of abaxial stereids, lumina small, walls strongly thickened, abaxial epidermal cells undifferentiated or 1–2 rows with lumina slightly enlarged, walls strongly thickened. Upper laminal cells chlorophyllose, ± isodiametric to subquadrate or short-oblong, slightly angular with rounded corners, 7–18(25) µm wide, 7–23(32) µm long, walls papillose with 2–8 papillae over lumina, papillae ± "c"-shaped in most, with very short, blunt branches, or (in Bryobrittonia) smooth, in transverse section walls thickened, bulge ± prominently on both surfaces, papillae consist of short, digitate clusters of basally hollow wall outgrowths; upper marginal cells in 1 row, lumina ovate, walls strongly thickened marginally, otherwise as laminal cells, or (in Bryobrittonia) in 1 row distally from near middle of leaf, lumina ± rhomboidal with upper corner free marginally, walls ± plane, bulge slightly in free corner, in 1–2 rows basipetally, lumina narrowly oblong, walls plane; transitional cells ± chlorophyllose, quadrate to oblong, walls thickened or (in few) slightly thickened or thin, on adaxial surface smooth well above basal cells or papillae extend almost to basal cells, papillae ± as on upper cells, on abaxial surface smooth well above basal cells or papillae extend to basal cells, papillae ± as on upper cells or enlarged, some "o"-shaped, much-branched, branches longer than on upper cells, papillae extend farther basipetally on abaxial than on adaxial surface, or (in *Bryobrittonia*) smooth, in transverse section walls ± thickened to (in *Bryobrittonia*) thin, bulge ± prominently as upper laminal cells to plane basipetally; *basal laminal cells* oblong to slightly irregularly oblong, (14)35-120(140) µm long, (7)12-23(30) µm wide, ± distinctly differentiated with transverse walls strongly thickened at corners, orange to dark-orange, yellow in few, entire or perforated by 1 large pore, superficial walls thin, hyaline to orange, smooth or (in 1 taxon) papillose abaxially, entire or irregularly perforated, or (in *Bryobrittonia*) less distinctly differentiated with walls hyaline to pale-orange or brown, transverse walls thin to (when older) slightly thickened, entire or irregularly perforated, longitudinal walls thin, entire, superficial walls thin, smooth, entire; *basal marginal cells* ± undifferentiated to ± distinctly differentiated, grade into laminal cells, cells faintly chlorophyllose, in 2-20 rows, narrowly long- to short-oblong, (2)5-7(9) m wide, walls smooth, longitudinal walls slightly thickened, transverse walls thin, perpendicular or slightly oblique to margin in outer row, upper corner free marginally in some. Goniautoicous, perigonia bud-like, short-stalked and lateral, closely associated with or just below perichaetia, attached to stem or base of costa, or (2 species) dioicous. *Perichaetial leaves* ± undifferentiated to ± differentiated by ± broad, sheath-like base, basal laminal cells less distinctly differentiated in some, otherwise as vegetative leaves; *perigonial leaves* distinctly differentiated, broad and sheath-like, 0.8-1.2(1.5) mm long, or (in *Bryobrittonia*) little differentiated to ± broad and sheath-like, 1.6-3.0 mm long; *perigonial paraphyses* with cells uniform in size or (in *Bryobrittonia*) upper 4-5 cells abruptly enlarged, upper cells entire or divided longitudinally in some, walls slightly thickened, smooth or with 1-3 low, rounded papillae on apical cells.

Seta 2-38 mm long, erect to flexuose, smooth, slightly twisted sinistrosely below or (in few) untwisted below, ± twisted dextrorsely near capsule, ± shiny to dull, orange to yellow, red or blackish; in transverse section rounded, 135-250 µm in diameter, central strand distinct, cells minute, parenchymatous, walls thin, centrifugally cells ± enlarged, walls thickened, outer cells smaller, walls strongly thickened. *Capsule* 1.0-4.3 mm long, erect, when dry cylindric to narrowly cylindric, and (in most) ± constricted beneath rim, neck indistinct or (in 2 species) ± well-differentiated, smooth, delicately striate or ± furrowed, furrows longitudinal or spiral, pale-brown, golden, yellow, orange or dark-red, some with red ribs, rim red or (in few) undifferentiated; when moist constriction beneath rim indistinct or absent; when old ± collapsed and split, ± furrowed in many, dull-orange to grey-brown; exothecial cells in ± regular, longitudinal or (in few) slightly spiral rows, ± irregular and short- to long-oblong, 40-200 µm long, 12-35 µm wide, shorter near capsule base and rim, in transverse section superficial and adjacent radial walls thin to ± strongly thickened; rim cells ± differentiated in 1-6 rows, quadrate, subquadrate or short-oblong, 5-30 µm long, 2.0-30 µm wide, walls thin to ± thickened; stomata superficial to (in 2 species) superficial or indistinctly immersed, sparse to ± numerous, restricted to capsule base or ± scattered, 30-70 µm long, 28-55 µm wide, subsidiary cells undifferentiated. Peristome absent in some, when present consists of either (a) 2 concentric layers, exostome teeth and endostome segments ± unfused, 16, opposite, to 1.2 mm long, exostome ± erect to (in 1 taxon) strongly recurved above, low basal membrane present or absent, teeth filiform, orange, ± smooth to ± papillose, papillae irregularly granular, outer surface with 2 vertical rows of cell plates, inner surface with prominent trabeculae, endostome erect, basal membrane well-developed, ca. 1/3 height of segments, pleated with revolute flanges on outer surface between segments, fenestrate or entire, segments filiform above, pale-orange, finely scabrous, outer surface with 1 vertical row of cell plates, inner surface with 2 vertical rows of cell plates at base of membrane; (b) 2 concentric layers, exostome teeth and endostome segments almost completely fused, 16, to 0.6 mm long, erect, slightly incurved or slightly reflexed, lanceolate-linear to linear-lanceolate, white, pink or crimson-red, exostome outer surface with 2 vertical rows of cell plates, densely papillose, papillae irregularly granular, or (exceptionally) ± smooth, inner surface with trabeculae fused to endostome, endostome segments ± joined laterally at base by very low membrane that extends to or only slightly above capsule rim, inner surface with 2 vertical rows of cell plates basally, densely papillose, papillae irregularly granular, or (exceptionally) ± smooth; or (c) 1 layer of 16 teeth, to 0.3 mm long, erect to reflexed or inflexed, lanceolate, dark-orange to (in few) hyaline, outer surface ± densely papillose, papillae irregularly granular, to (in few) sparsely scabrous or irregular, with 1 row of cell plates, inner surface smooth, with 2 rows of cell plates at base of tooth, preperistome absent or (in few) present and consists of 2 rows of cell plates. Operculum conic-rostrate, convex-rostrate or concave-plane rostrate, 0.1–2.5 mm long, 1–2 lowest rows of cells differentiated ± as capsule rim cells. Annulus undifferentiated in most, when present prominent, glossy and crimson-red, massive, deciduous in large fragments, 3 rows of cells, outer walls thickened, opaque, inner walls thin, transluscent, when wet cells inflated radially and periclinally. Spores olive-green, orange or dark-brown, atreme or possibly katalept, few with distinct trilete aperture, spherical to elliptical and isopolar, or circular in polar view but ± concave- or plane-convex in lateral view and paraisopolar to heteropolar, 7–80 μ m, exospore structure intectate and scabrate, verrucate, gemmate or vermiculate, processes 0.25–8 μm in diameter, up to 40 μm long, exospore sculpture rugulate, striate or reticulate in some. Calyptra long-mitrate, rostrate, extends well below capsule or (in few) to capsule base, 2–10 mm long with rostrum 0.5–2.3 mm long, cylindric to elliptic-cylindric, smooth to scindulose or papillose, smoky-brown, golden-brown, golden or pale golden, opaque to ± transparent, shiny to dull; in transverse section of cylinder 3–5 rows of cells with small lumina, walls very thick, 1–2 innermost rows with enlarged lumina, walls thinner and mostly ± collapsed. Chromosome number n=13 or 26 in most, fewer with n=12, 14, 27, 39 or (in Bryobrittonia) 52.

CONSPECTUS OF GENERA OF ENCALYPTACEAE

1. Upper laminal cell walls smooth; leaf margins crenulate in upper half; upper marginal cells in 1 row distally from near middle of leaf, rhomboidal with upper corner free marginally, in 1–2 rows basipetally, narrowly oblong; basal laminal cells with transverse walls thin or slightly, evenly thickened, longitudinal walls thin or slightly evenly thickened; perigonial paraphyses with upper 4–5 cells abruptly enlarged . . . . **Bryobrittonia** (p.).

1. Upper laminal cell walls papillose with digitate clusters of walls outgrowths over lumina; leaf margins entire in upper half; upper marginal cells in 1 row, lumina ovate to subquadrate, walls strongly thickened marginally; basal laminal cells with transverse walls ± strongly thickened, particularly at corners, longitudinal walls thin; perigonial paraphyses with cells uniform in size . . . . **Encalypta** (p.).

The Encalyptaceae have generally been considered a monotypic family. There are a few exceptions, for example Limpricht (1890) included *Merceya* and Müller (1901) included *Streptocalypta*, but these genera lack the distinctive, encalyptaceous calyptra. When Steere found the first population of *Bryobrittonia* with sporophytes in 1952, the shape of the calyptra left no doubt as to the affinities of the genus (Steere 1953), which had formerly been placed in the Pottiaceae (Brotherus 1924, Grout 1939). Furthermore, Steere (1953) reported that "There exists no single important character or group of characters in the sporophyte of *Bryobrittonia* that can be used to distinguish it from the diplolepidous species of *Encalypta*;...". Indeed, in features of the capsule, peristome, seta and spores, in addition to the calyptra, *Bryobrittonia* is more similar to both *E. streptocarpa* and *E. procera* than they are to some other species of *Encalypta*. Such pronounced similarity in characters that are generally a reliable basis for the delimitation of moss genera brings into question the validity of recognizing *Bryobrittonia* as a genus distinct from *Encalypta*.

I would agree with Steere (1947) that whenever possible generic concepts in the Musci should be based upon a combination of both sporophytic and gametophytic features. However, the remarkable variation in structure of the sporophyte, particularly the peristome, in species of *Encalypta* precludes definition of the genus on this basis. The characteristics that link species of *Encalypta* are all gametophytic, the most prominent of these being the entire leaf margins, papillose upper leaf cells with thickened transverse walls, as well as the basic shape of the calyptra. On the basis of these gametophytic character-states alone, species of *Encalypta* form a natural group. While *Bryobrittonia* is characterized by the same calyptra-type and there is a fundamental structural similarity between the upper laminal cells of species of *Encalypta* and those of *Bryobrittonia* (Horton 1979a), *Bryobrittonia* is well differentiated by the crenulate upper leaf margins, smooth upper leaf cells and basal cells with the transverse walls thin or only slightly thickened as are the longitudinal walls.

Horton (1979a) reported an aberrant population of *E. spathulata* with more-or-less smooth upper leaf cells and suggested that this indicates "...a potential within the genus *Encalypta* for the differentiation of leaves with smooth, bulging upper leaf cells,..." like those of *Bryobrittonia*. This might be regarded as evidence that the differences between *Bryobrittonia* and species of *Encalypta* are not sufficiently stable to warrant recognition of *Bryobrittonia* as a separate genus. However, this is the only population of an *Encalypta* species that I have seen with this condition and therefore probably should not be accorded undue significance. *Bryobrittonia* is so divergent from all species of *Encalypta* in the gametophytic character-states described above, as well as others, and these differences are stable under natural conditions (with the single exception cited above) that there can be no doubt that the two ought to be regarded as separate genera, as Steere (1953) concluded. Clearly, the calyptra is the defining feature of the family Encalyptaceae.

BRYOBRITTONIA Williams

Bull. New York Bot. Gard. 2: 115, pl. 16, figs. 1-8. 1901.

The genus *Bryobrittonia* is monotypic; therefore, it is treated together with the species, *B. longipes*.

BRYOBRITTONIA LONGIPES (Mitten) Horton,

Brittonia 30: 19, pl. 5, figs. 1-4. 1978.
Figs. 1, 15, 18-19, 21, 23, 33, 55-57, 65, 80-94.

Basionym: *Encalypta longipes* Mitt., J. Proc. Linn. Soc., Bot. 8: 29. 1864. Type: "In a shaded place by the side of a rivulet, Rocky Mountains, Drummond." (Lectotype: "Nr.435 Encalypta streptocarpa [?]ar. side of a rivulet Rocky Mountains stem short fruit stalks long in proportion growing in a shady place Drummond." NY-Mitt.!, Isotype: NY-Mitt.!; Possible Isotype: E (in part)!).

Bryobrittonia pellucida Williams, Bull. New York Bot. Gard. 2: 115. 1901. Type: "Yukon River bluff, just below Dawson. Collected April 6, 1899, on rock (587)." (Holotype: "587. Bryobrittonia pellucida R. S. Williams April 6, 1899. On rock. Dawson." NY!).

Nomenclatural Notes: (1) The discovery that the type of E. longipes is actually a specimen of Bryobrittonia, which was described by Williams in 1901, was reported by Horton (1978) and the new combination B. longipes was made. Horton also discussed the taxonomic confusion generated by Mitten's (1864) erroneous description of the upper leaf cells of his E. longipes as papillose, and the fact that a number of people, including E. G. Britton, considered Drummond's Musci Americanae Number 48 to be a specimen of E. longipes. In reality, Number 48 is E. procera; therefore, E. longipes was dismissed as a synonym of E. procera (Britton in Coker 1918, Lesquereux & James 1884, Macoun & Kindberg 1892).

However, an isotype of E. longipes from Sullivant's herbarium (NY!) that I had not seen when I published the information summarized above (Horton 1978) is of considerable historical interest as it establishes beyond doubt that Britton did see authentic material of E. longipes and furthermore that she recognized some of the essential features that differentiate Bryobrittonia from all species of Encalypta. On the outer packet of this specimen in Sullivant's herbarium is the notation "Type from Mitten's set in hb. Sullivant Jany. 1891." and the inner packet bears the title "Revision of N.A. Mosses, by E. G. Britton.". The inside of this packet has a tracing of Mitten's original illustrations and along either side are notes on the plants (which are contained in a mica slide and tissue paper) written by E. G. Britton. The critical features that distinguish the genus Bryobrittonia from Encalypta are noted, including the minutely erose upper leaf margins, "Cells not papillose but mamillate!" (an obvious reference to Mitten's original description of the upper laminal cells as papillose) and the strikingly long seta ("2 1/2 cm! a little less than '1.5 inches'"). Other observations included notations that the abaxial surface of the costa is smooth, the calyptra is smooth throughout and "I think I can see traces of ridges on walls of young capsule!".

Britton (1895) discussed the taxonomic status of E. longipes in a short paper in the series "Contributions to American Bryology". The original Latin description of E. longipes was cited, as was a portion of Mitten's English discussion of his new species that read "Seta an inch and a half long, slightly flexuose. Capsule too immature to show if it is furrowed.". She then quoted Lesquereux and James' (1884) discussion of E. longipes with their assertion that they had examined all specimens of E. longipes in Drummond's sets (a reference to his *Musci Americanae* exsiccata) and conclusion that *E. longipes* is synonymous with *E. procera*. In contrast, Britton stated that she had examined the type of *E. longipes* in Mitten's herbarium at Cambridge (no mention was made of the specimen from Sullivant's herbarium with her notations on it - possibly a "kleptotype"?) and that "We can corroborate Mitten's statements, with additional evidence that this is not the same species as *E. procera*". A discussion of the features noted above follows, with the correction of Mitten's misinterpretation of the upper leaf cell structure, but she followed his analysis of the peristome and reported it to be single. The relevance of the references to smooth costa and calyptra becomes obvious in the light of a comparison with *E. procera*, which is characterized by a papillose costa and a more-or-less scabrous calyptra. Britton also pointed out that in spite of Kindberg's (Macoun & Kindberg 1892) contention that he had examined authentic specimens of *E. longipes* in C. Müller's herbarium, he in fact could not have, as his description of the costa and calyptra were a direct contradiction of what she had seen.

Therefore, it seems very likely that the confusion of both Kindberg, and Lesquereux and James arose as a result of Drummond's *Musci Americanae* No. 48. In view of her statement that *E. longipes* is distinct from *E. procera*, it is confusing that in Coker's revision of *Encalypta* in North America Britton (Coker noted in the introduction that the synonymy was primarily Britton's work) placed *E. longipes* in synonymy with *E. procera*. However, the basis for this apparent change of opinion may be inferred from one of Britton's concluding statements in the earlier paper (Britton 1895): "We do not like to venture an opinion without careful comparisons, especially as this species is so meagrely represented in the type, which is also immature, so that it is rather unsatisfactory for purposes of comparison;...". It is a pity that E. G. Britton never associated *E. longipes* with her namesake, *Bryobrittonia*.

(2) When I published the new combination of *B. longipes* in 1978 (Horton 1978), I was unaware that there is more than one original specimen of *B. longipes* in Mitten's herbarium. Therefore, I indicated that the type specimen is a holotype (Horton 1978). Since then the duplicate specimen has come to my attention. As it is almost certain that the original description was based upon both of these specimens, the specimen previously cited as the holotype is here designated the lectotype.

(3) There is a specimen in E with the label information "Encalypta procera Br. & Sch. Rocky Mts. N. America G. J. Lyon 1846". All of the plants, except one, consist of E. procera with sporophytes and this one is a plant of B. longipes with a sporophyte. I am unaware of the existence of any specimens of Bryobrittonia that were collected prior to the end of the 19th century besides that collected by Drummond (that is, the type of E. longipes). Therefore, I suspect that this one plant probably was a part of that original collection.

Diagnosis and Differentiation: Bryobrittonia longipes is characterized by bright-green, dull plants with incurved leaves that have a prominent, shiny costa and involute margins. In the field a distinctive golden sheen can be seen on the leaves with a hand lens when the plants are moved so that they catch the sunlight. The leaves are mostly elliptic-oblong or ovate-oblong with an acute apex, the margins are finely crenulate in the upper half (a feature readily apparent only with the compound microscope) and the smooth upper laminal cell walls bulge prominently on both surfaces. Generally, populations of B. longipes lack sporophytes, but when they do occur the exceptionally long, flexuose and black or reddish-black seta is an unmistakable characteristic. Also, the smoky-brown color of the calyptra is distinctive and the cylinder is tapered distally so that the rostrum is not distinctly defined. Other important features of the sporophyte include the capsule with longitudinal furrows, the long peristome consisting of two almost unfused layers with the dark-orange exostome teeth opposite the paler endostome segments that are joined by a well-developed basal membrane, the massive annulus that is glossy crimson-red, and the long-conic rostrum that is nearly the same length as the capsule. The olive-green spores are small, isopolar and finely scabrous or scabrous-rugulate. In some populations, the rugulae form a distinctive 'fingerprint' pattern, but this detail is discernible only with the SEM.

Plants of Bryobrittonia with sporophytes are seldom found. Therefore, differentiation from species of Encalypta must generally be made on the basis of the vegetative plants. A characteristic of Bryobrittonia that I have observed but rarely in a few species of Encalypta is that the leaf laminae are inrolled when dry so that the margins are not visible. The most distinct differences between Bryobrittonia and species

Figures 80-85. Bryobrittonia longipes. Scale=1 mm.

Fig. 80. Habit of plant with sporophyte.

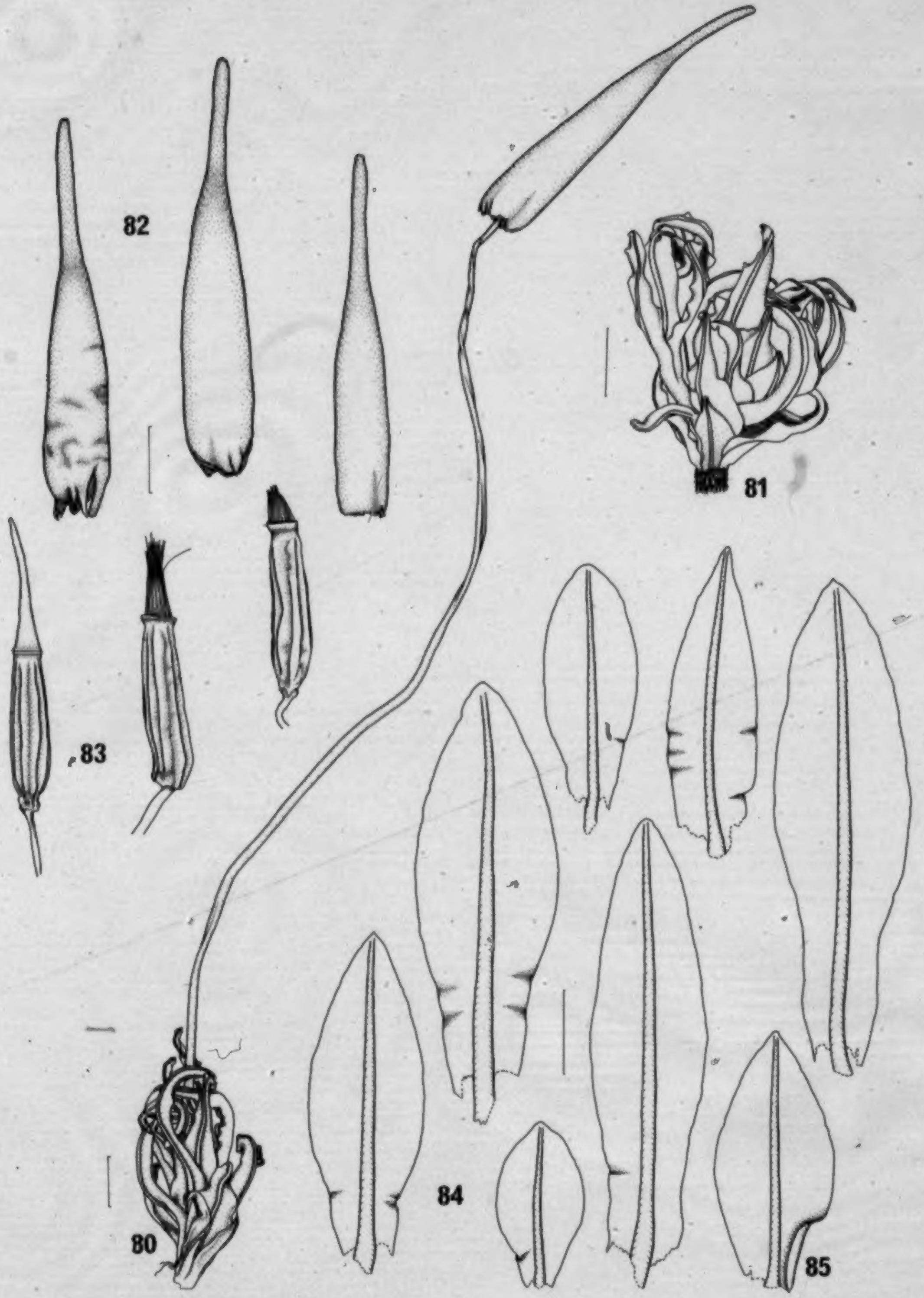
Fig. 81. Habit of perigonial plant. Note subterminal innovation and scale leaves (left).

Fig. 82. Calyptrae.

Fig. 83. Capsules.

Fig. 84. Vegetative leaves.

Fig. 85. Perichaetial leaves.



Figures 86-91. ***Bryobrittonia longipes.***

Fig. 86. Peristome. Scale=400 µm.

Figs. 87-91. Variation in Spore Size and Structure.

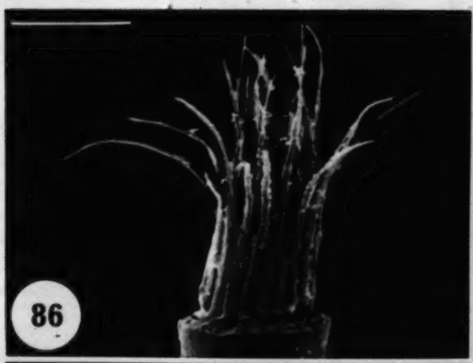
Fig. 87. Scale=10 µm.

Fig. 88. Scale=4 µm.

Fig. 89. Scale=2 µm.

Fig. 90. Scale=4 µm.

Fig. 91. Scale=10 µm.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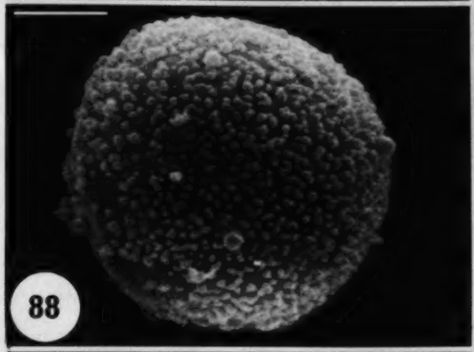
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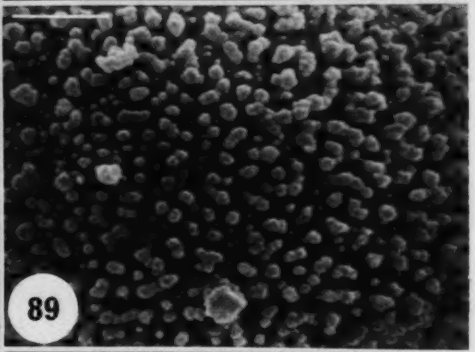
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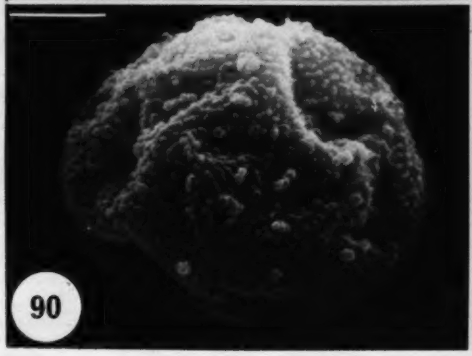
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91

of Encalypta are microscopic. Upper leaf cell structure is so different from that of all Encalypta species that Bryobrittonia is not likely to be confused with these. The leaf margins of all Encalypta species are entire, and the upper laminal cell walls not only bulge as they do in Bryobrittonia, but they are also further elaborated by digitate clusters of wall outgrowths that form the more-or-less "c"-shaped papillae. Furthermore, in species of Encalypta a single row of upper marginal cells is differentiated. The lumina of these are ovate to subquadrate in shape, while in Bryobrittonia, in the upper half of the leaf, there is one row of more-or-less rhomboidal cells with the upper corner free marginally in the upper half of the leaf. Proximally, there are one to two rows of narrowly oblong cells that form a narrow, shiny border visable with a stereoscope. These cells grade into the basal marginal cells.

When sprophytes occur, plants of Bryobrittonia are most apt to be confused with E. streptocarpa or E. procera. The calyptra rostrum of E. streptocarpa is ill-defined as is that of Bryobrittonia, and coloration of the calyptra is very similar in these two species. The cylinder of the calyptra tends to be longer and narrower in E. streptocarpa, otherwise, these two species are very difficult to differentiate on the basis of calyptra character-states. The capsules of E. streptocarpa are spirally furrowed, and the seta is shorter than that of Bryobrittonia. The rostrum of the calyptra of E. procera is, in most populations, slightly, but distinctly narrowed from the cylinder, and the calyptra is golden in color. The North American populations of E. procera are differentiated by spirally furrowed capsules, but capsules with longitudinal furrows characterize some of the Scandinavian populations and these might be confused with Bryobrittonia. As with E. streptocarpa, the seta of E. procera is generally shorter than that of Bryobrittonia. Both E. streptocarpa and E. procera are best differentiated by the vegetative characteristics noted above. As well, the upper leaves of sporophytic plants of E. procera are hair-pointed.

Sterile populations of Bryobrittonia are more likely to be confused with such other mosses as Barbula convoluta Hedw. and Timmia norvegica Zett. or T. sibirica Lindb. et H. Arnell that occur along rivers or streams, as is characteristic of Bryobrittonia. Plants of Barbula convoluta superficially resemble those of Bryobrittonia in the bright-green coloration; however, in the Barbula there is always a distinct bright-yellow tone that does not occur in *Bryobrittonia*. Also, plants of *B. convoluta* are smaller than those of *Bryobrittonia*, but they are best differentiated by the revolute leaf margins that are visible with a hand lens. Steere (1953) first drew attention to the "...very decided resemblance..." between *Bryobrittonia* and species of *Timmia*, "...especially to juvenile forms of *T. norvegica*". The habit of plants of *T. norvegica* and *T. sibirica* is so similar to that of *Bryobrittonia* that these species are, on occasion, virtually indistinguishable in the field and difficult to differentiate even with a dissecting microscope. Both species of *Timmia* are characterized by bright-green, unbranched plants. When moist and fresh, the upper surface of the laminae has the same golden sheen so characteristic of *Bryobrittonia*. When dry the spreading leaves are more-or-less incurved and twisted in the upper part, and the costa is prominent and more-or-less shiny. *Timmia norvegica* is perhaps most confusing because the laminae are involute just as in *Bryobrittonia*, but the abaxial surface is smooth whereas the bulging cells of *Bryobrittonia* are visible with a stereoscope. The papillose laminal cells of *T. sibirica* give it a velvety appearance similar to that of *Bryobrittonia*, but the laminae are incurved, not involute, revealing irregularly serrate margins and a narrow shiny border that extends right to the tip of the leaf. Another feature that differentiates both these species from *Bryobrittonia* is the long, sheathing leaf bases that result in more distant spacing of the leaves along the stem and more elongate habit of the plants. The leaves of *Bryobrittonia*, which lack such pronounced sheathing bases, are more crowded and the plants therefore appear denser.

Description: *Plants* to 25 mm tall, bright-, golden- or olive-green to blackened above, dark-brown to blackened below; unbranched. *Stem* in transverse section with central strand distinct. *Brood bodies* absent. *Axillary hairs* abundant, in rows of up to 12 filaments joined laterally below, covered by gelatinous substance, up to 2 mm long, hyaline, thin-walled, unbranched, attached to leaf bases and stem. *Leaves* when dry with apices incurved to loosely spread, ± twisted, laminae involute to inflexed, slightly reflexed in a few populations, ± undulate; when moist erect-spread, laminae inflexed to plane; (1.6)3.0-6.5(8.0) mm long, 1.0-2.0 mm wide, elliptic-oblong or obovate-oblong to ovate-oblong, apex ± acute to obtuse, muticous, blackened in many populations; *margins* plane, crenulate in the upper half. *Costa* ends 2-5 cells below apex, abaxial surface prominently keeled, shiny and smooth, transluscent-green, adaxial surface with smooth laminal-type cells above; in transverse section 3–4 rows of ventral cells, begleiters distinctly differentiated in small central cluster, lumina minute, walls thin, 2–3 rows of abaxial stereids, 1–2 rows of abaxial epidermal cells with lumina slightly enlarged, walls strongly thickened. *Upper laminal cells* (9)14–23(25) μm wide, (9)12–23(32) μm long, walls smooth; in transverse section walls bulge prominently and roundly on adaxial surface, bulge less with slight but ± distinct contraction in upper part on abaxial surface; *upper marginal cells* in 1 row distally from near middle of leaf, lumina rhomboidal with upper corner free marginally, walls ± plane, bulge slightly in free corner, in 1–2 rows basipetally, lumina narrowly oblong, walls plane; transition to basal cells gradual, cell walls thin to slightly thickened, smooth; *transitional cells* with walls smooth, in transverse section walls thin to somewhat thickened, bulge ± prominently as upper laminal cells to plane basipetally; *basal laminal cells* 35–140 μm long, 14–30 μm wide, walls thin or transverse and longitudinal walls slightly thickened in older leaves, smooth, hyaline to pale-orange in most populations, brownish in older leaves and then form ± distinct group, extend diagonally from costa to margins, transverse walls entire or irregularly perforated, longitudinal walls entire, superficial walls entire; *basal marginal cells* ± undifferentiated in color, narrower than basal laminal cells, in 4–7 rows. Dioicous, perigonial plants rare. *Perichaetial leaves* little differentiated from vegetative, somewhat smaller in most populations, elliptic-oblong to elliptic-ligulate; *perigonial leaves* (1.7)2.0–3.0 mm long, undifferetiated to ± broadly ovate to obovate, acute; margins entire but slightly irregular; *perigonial paraphyses* with upper 4–5 cells abruptly enlarged, entire or divided longitudinally in some, walls slightly thickened, smooth.

Seta (12)20–30(38) mm long, flexuose, stout below, tapered distally, smooth and rounded, laxly twisted sinistrorsely below, ± twisted dextrorsely near capsule, dull, blackish to reddish-black, and (in most) pale-yellow near capsule; in transverse section 230–250 μm below. *Capsule* (1.5)2.0–3.0 mm long, when dry cylindric, broadest basally and slightly tapered to mouth, to cylindric, ± deeply longitudinally furrowed, slightly constricted beneath rim, ± puckered basally and abruptly contracted to seta, dull-golden or green with dull-orange rim, dark-reddish basally, when old ± collapsed or ± inflated, some ± curved; *exothecial cells* 41–104 μm long, 9–21 μm wide, in longitudinal rows, in transverse section superficial and adjacent radial walls somewhat thickened, 6 μm thick on superficial walls; rim cells in 1-2 irregular rows, irregularly quadrate, 12-14 μm wide, 12-14 μm long, walls strongly thickened, opaque; stomata superficial to indistinctly immersed, 12-15, restricted to capsule base, 35-37 μm long, 32-55 μm wide. Peristome 0.8-1.2 mm long, when old ± broken off, in 2 concentric layers, exostome teeth and endostome segments ± unfused, 16, opposite, exostome ± erect, longer than endostome, low basal membrane present, teeth filiform, dark-orange below, paler distally, ± smooth to densely irregularly papillose, outer surface with 2 vertical rows of cell plates, inner surface with prominent trabeculae; endostome erect, basal membrane well-developed, 1/3 height of segments, pleated with revolute flanges on outer surface between segments, fenestrate or entire, segments filiform above, pale-orange, finely papillose, outer surface with 1 vertical row of cell plates, inner surface with 2 vertical rows of cell plates at base of membrane; preperistome absent. Operculum conic-rostrate, 1.9-2.5 mm long. Annulus prominent, glossy and crimson-red, massive, ± deciduous in large fragments, 3 rows of cells, outer walls thickened, opaque, inner walls thin, transluscent, when wet cells inflated radially and periclinally. Spores olive-green, circular to elliptical, isopolar, (7)12-18(25) μm, of variable size within individual capsules, larger ones chlorophyllose, most turgid, some ± collapsed, smaller ones brown, collapsed, few chlorophyllose, minutely scabrate or scabrate-rugulate, scabrae 0.25-0.50 μm, rugulae up to 2 μm long, extraneous deposition of slightly larger granules superimposed sporadically over surface. Calyptra 4-8 mm long, extends well below capsule, cylindric, ± tapered distally to erect or slightly curved rostrum that is 1.5-2.0 mm long, cylinder basally incurved and slightly puckered, ± erose to lacerate, calyptra smoky-brown, opaque, shiny or dull, smooth to moderately scindulose in rostrum, scindulae rounded, smooth below; in transverse section of cylinder 4-5 rows of cells with small lumina, walls very thick. Chromosome numbers n=13, 26 (Inoue 1974) and 52 (Lazarenko 1967).

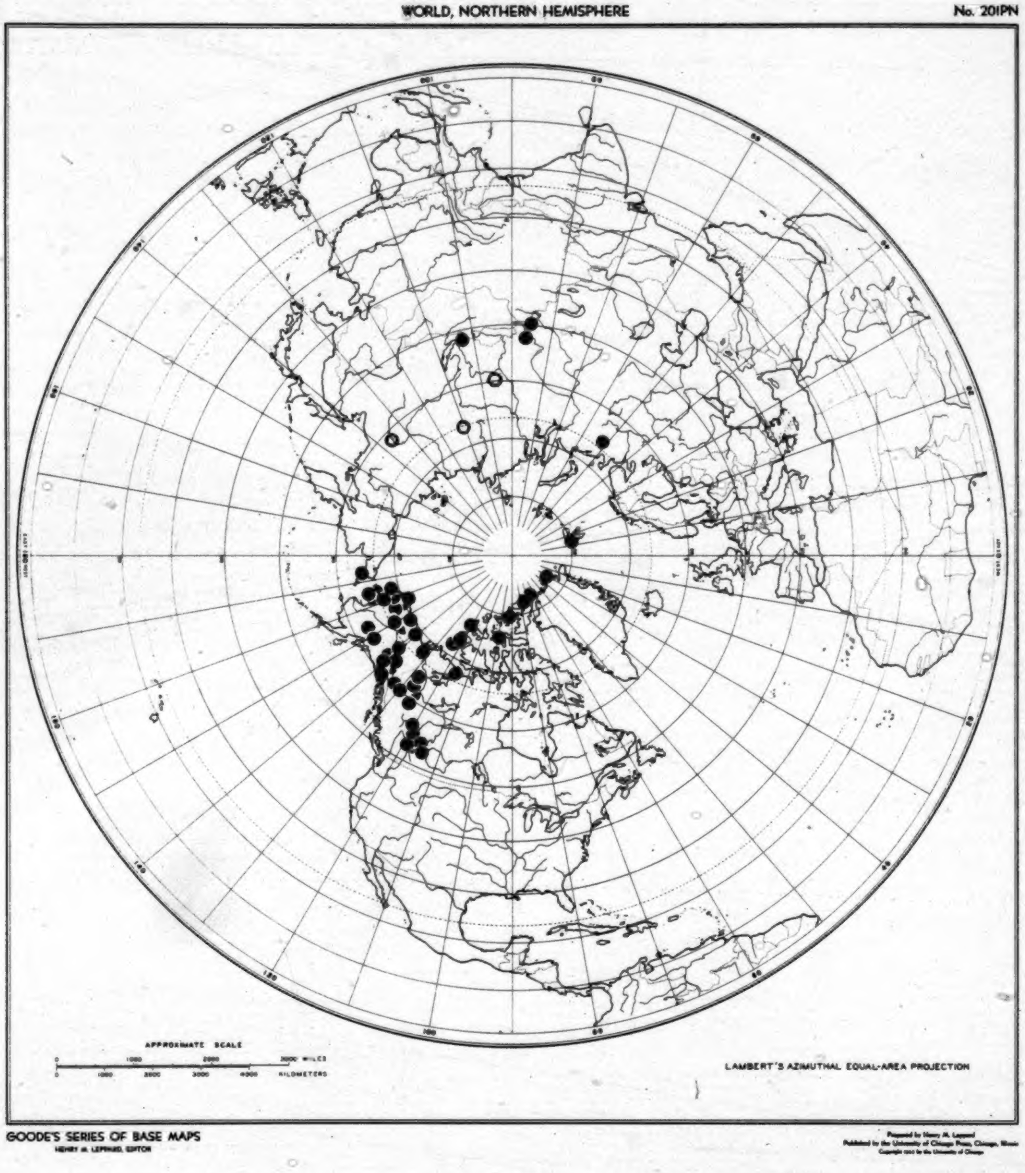
Habitat: Populations of B. longipes grow primarily in montane and tundra habitats. Most occur along streams or rivers. In such habitats the plants occur close to the water, frequently on the overhanging banks, on fine, silty or sandy soil and generally intermixed with other bryophytes that are similarly characteristic of this habitat. These associates include *Blepharostoma trichophyllum* (L.) Dum., *Dicranella grevilleana* (Brid.) Schimp., *D. schreberiana* (Hedw.) Schimp., *Distichium inclinatum* (Hedw.) B.S.G., *Encalypta procera*, *Leptobryum pyriforme* (Hedw.) Wils., *Orthothecium chryseum* (Schwaegr. *ex* Schultes) B.S.G., *Pohlia vexans* (Limpr.) H. Lindb. and *Timmia norvegica*. In the course of work on the North American propaguliferous species of *Pohlia*, J. Shaw has also found *Bryobrittonia* to be a particularly consistent associate of *P. vexans* (*pers. comm*). Some of the populations of *B. longipes* are shaded by *Salix* and *Betula* shrubs, others are found in unshaded habitats. *Bryobrittonia* also occurs, but seldom, on ledges or in crevices of rock outcrops in montane forests or alpine and arctic tundra; these populations generally are pure and consist of few plants. In the northern part of its North American range in Alaska-Yukon, *B. longipes* is also found in alpine tundra on exposed soil around the mouth of abandoned ground squirrel holes, on steep talus slopes on the vegetation stripes, and on soil along the edge or in the channel of seasonal streamlets. In such habitats, *B. longipes* forms pure popuations or is intermixed with *Arnellia fennica* (Gott.) Lindb., *Bryoerythrophyllum recurvirostrum* (Hedw.) Chen, *Bryum inclinatum* (Sw. *ex* Brid.) Bland. *in* Sturm, *Cinclidium arcticum* Schimp., *C. latifolium* Lindb., *Cyrtomnium hymenophyllum* (B.S.G.) Holmen, *C. hymenophylloides* (Hüb.) Kop. and *Tomenthypnum nitens* (Hedw.) Loeske. The most luxuriant, fruiting population of *Bryobrittonia* that I have seen (to be distributed in the *Encalyptaceae Americanae Exsiccatae* - see Horton 1979a) was collected in the Mackenzie Mountains at the base of a steep slope in an herb field with *Epilobium angustifolium* L., *Petasites frigidus* (L.)Franch., *Salix* spp. and *Senecio triangularis* Hook. The plants of *B. longipes* were growing on gravelly ridges that appeared to have built up along the edge of seasonal water channels. The herbaceous growth was not quite as dense on top of these ridges where the *Bryobrittonia* was growing, but the plants were intermixed with *Equisetum scirpoides* Michx. and grasses. *Bryobrittonia* has also been collected in mesic, roadside ditches and even on the soil clinging to the base of an uprooted tree.

Bryobrittonia is probably a distinct calciphile. The underlying substrate at the localities where populations have been collected is always calcareous; most often it is limestone. In western North America, the pH of the soil on which populations from

Alberta, British Columbia and the Yukon Territory were growing ranged from 6.6 to 7.6 (n=14 from 4 different localities) with a mean of 7.1 (s.d.=0.42) (Fig. 300). The recording of pH 6.6 is anomalous considering the rather consistent association of *Bryobrittonia* with limestone. It may indicate a tolerance of subneutral substrates, but more data are needed to verify such a suggestion. All of the associated species listed above are known to occur on highly calcareous substrates, even if not all are considered to be as narrow in their range of tolerance as is *Bryobrittonia*. However, *Bryobrittonia* is quite different than the species of *Encalypta* that are restricted to substrates with a high pH in that the Ca^{++} and Mg^{+} content of the soil is contrastingly low (Figs. 301-302,Table 9). Possibly this reflects a more specialized habitat, which further studies might elucidate.

Distribution: *Bryobrittonia longipes* has a circumpolar montane-arctic distribution (Fig. 92). In North America, most collections are from the Western Cordillera. It is reported from Alaska in the Brooks and Alaska Ranges; from the Yukon Territory in the British, Ogilvie and St. Elias Mountains, and from lowland localities along the Alaska Highway between Watson Lake and Dawson; from the western Northwest Territories in the Nahanni Range of the Mackenzie Mountains; and from British Columbia and Alberta in the Rocky Mountains. The most southerly locality is in the Prairie Creek area just west of Rocky Mountain House in Alberta (52°N). *Bryobrittonia* is also reported from scattered localities in the Canadian Arctic including the Mackenzie Delta and Coppermine, as well as from the Arctic Archipelago on Banks, Prince Patrick, Bathurst, Axel Heiberg and Ellesmere Islands. On Greenland, *B. longipes* is known from Peary Land (Fig. 93). Elsewhere, *Bryobrittonia* is reported from Svalbard, and in Asia from Lake Baykal, in the Altai Mountains from Teletskoye Lake and the Katun River near Barangol, in the Komi A.S.S.R. from Ust'Tsil'ma, and from Lavrentiya on the Chukotskiy Peninsula (Fig. 92). Abramova and Abramov (1966) cited other collections from the region of the Lena River in Yakutsk A.S.S.R. at the headwaters of the River Markha and in the Verkhoyanskiy Range at the mouth of the Amga River, and from central Asia in the Krasnoyarsk region on the Yeniseyskiy Ridge (indicated on Fig. with open circles), but I am unable to confirm these reports as specimens have not been made available to me.

Figure 92. Distribution of *Bryobrittonia longipes*.


WORLD, NORTHERN HEMISPHERE
No. 201PN
APPROXIMATE SCALE
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0 1000 2000 3000 4000 KILOMETERS
LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION
GOODE'S SERIES OF BASE MAPS
HENRY M. LEPPARD, EDITOR
Prepared by Henry M. Leppard
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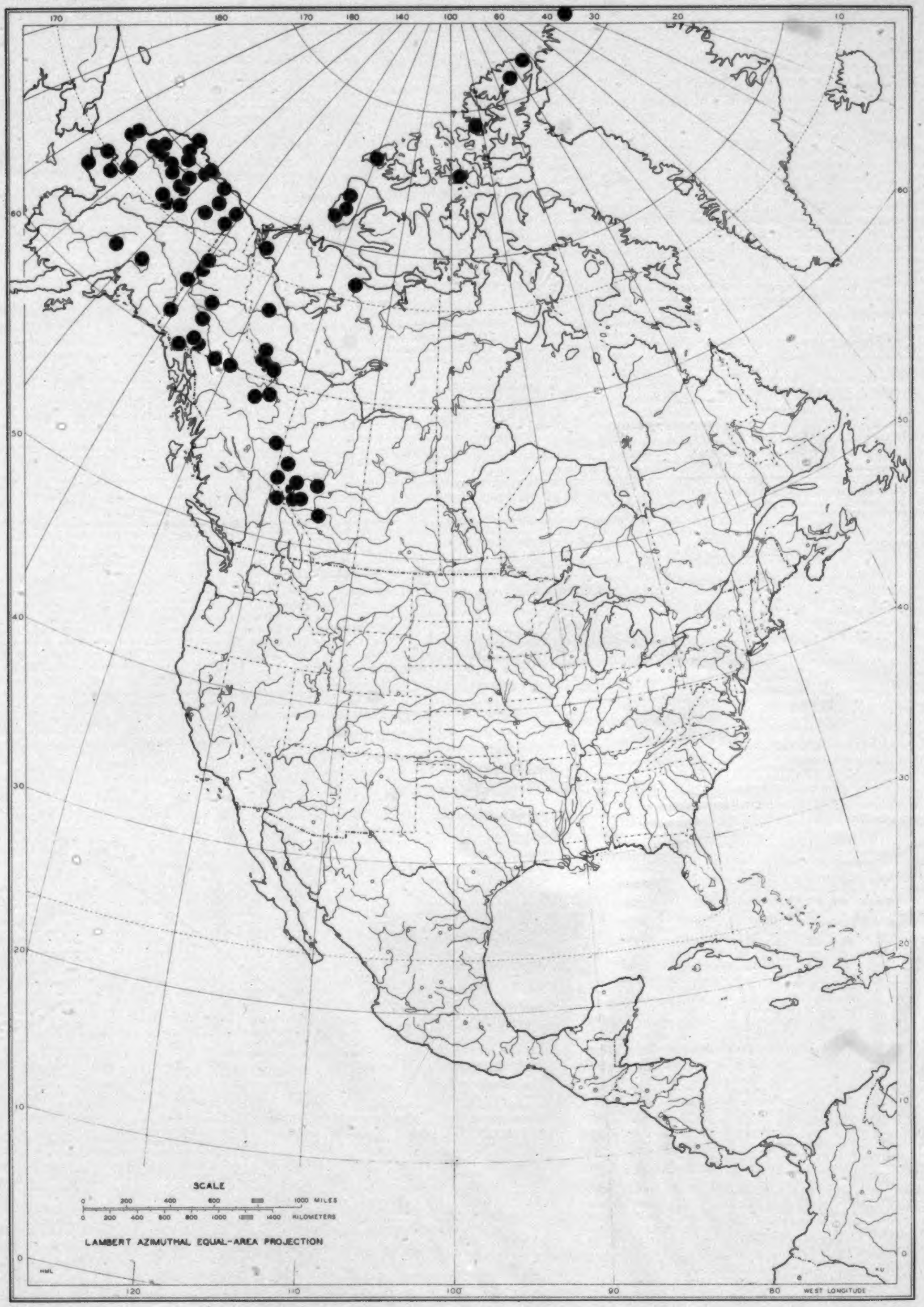
Figure 93. Distribution of *Bryobrittonia longipes* in North America.

NORTH AMERICA No. 2


SCALE
0 200 400 600 800 1000 MILES
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LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
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160
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120
100
80
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80
WEST LONGITUDE

GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

Prepared by Henry M. Leppard
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In western North America, *Bryobrittonia* is rare, but appears to be of sporadic occurrence in the Western Cordillera. The populations are very seldom extensive and most consist of just one or two plants. *Bryobrittonia* is not yet known from continental Europe, but will soon be reported from Svalbard (Frisvoll *pers. comm.*). Relictual populations may be found in Scandinavia and possibly in the Alps, but *Bryobrittonia* appears to have been all but eliminated in Europe. Judging by the widely scattered Asian localities, it is perhaps of more frequent occurrence and probably has a sporadic distribution from the Altai Mountains northward, eastward and westward across Siberia to the Urals.

In western North America, the distribution of *B. longipes* is a classic example that illustrates how our knowledge of the bryoflora of the Western Cordillera has changed over the last six years. When Vitt (1974) reported its distribution, *B. longipes* (as *B. pellucida*) was known from scattered localities in Alaska, the Yukon and Northwest Territories with a single southerly locality disjunct in the Grande Cache region of western Alberta. Vitt (1974) considered this range in the largely unglaciated regions of Alaska-Yukon and the disjunction to western Alberta to be further evidence supportive that some plants survived Wisconsin glaciation *in situ* in the southern Canadian Rocky Mountains. *Bryobrittonia* is now known to have a more-or-less continuous distribution in the Western Cordillera (Fig. 93). However, this does not necessarily negate the idea that populations survived glaciation in southerly refugia, as discussed in Horton (1981a). Some of the localities east of the Rocky Mountains that *Bryobrittonia* is now known from, for example the Genesee and Devon localities near Edmonton, probably do represent post-glacial dispersal along major river systems. But it is noteworthy that *Bryobrittonia* has not yet been found farther south in the Canadian Rockies in the Banff or Kananaskis areas where there are suitably calcareous habitats. It appears that *B. longipes* has limited potential for dispersal.

Structural Variation: Preliminary observations indicate that there are some irregularities in spores of *Bryobrittonia*. The basis for these observations are analyses of spores obtained from individual capsules in populations from the following localities: CANADA. British Columbia-Yukon Territory border: west of Watson Lake, 60°00'N 129°03'W,

Horton 9685 (ALTA - 1 capsule) (Fig. 94 - d). Northwest Territories: Logan Mtns., 62°34'N 128°31'W, Horton 14481 (ALTA - 3 capsules) (Fig. 94 - b, e, h). Yukon Territory: Clinton Creek, 64°37'N 140°37'W, Vitt 10747 (ALTA - 1 capsule) (Fig. 94 - a). U.S.A. Alaska: Brooks Range, Franklin Mtns., 69°22'N 145°03' W, Steere 18628 (ALTA - 1 capsule (Fig. 94 - f), NY - 1 capsule (Fig. 94 - i)); 69°19'N 145°02'W Steere & Iwatsuki 74-790 (NY - 1 capsule) (Fig. 94 - j), Steere 72-480 (NY - 1 capsule) (Fig. 94 - c). U.S.S.R. Irkutsk: western Sayan Riv., Bardunov 8.7.68 (ALTA 1 capsule) (Fig. 94 - g). (These specimens represent almost all of the populations of Bryobrittonia with sporophytes that have been found up to the present time, in the herbaria made available to me).

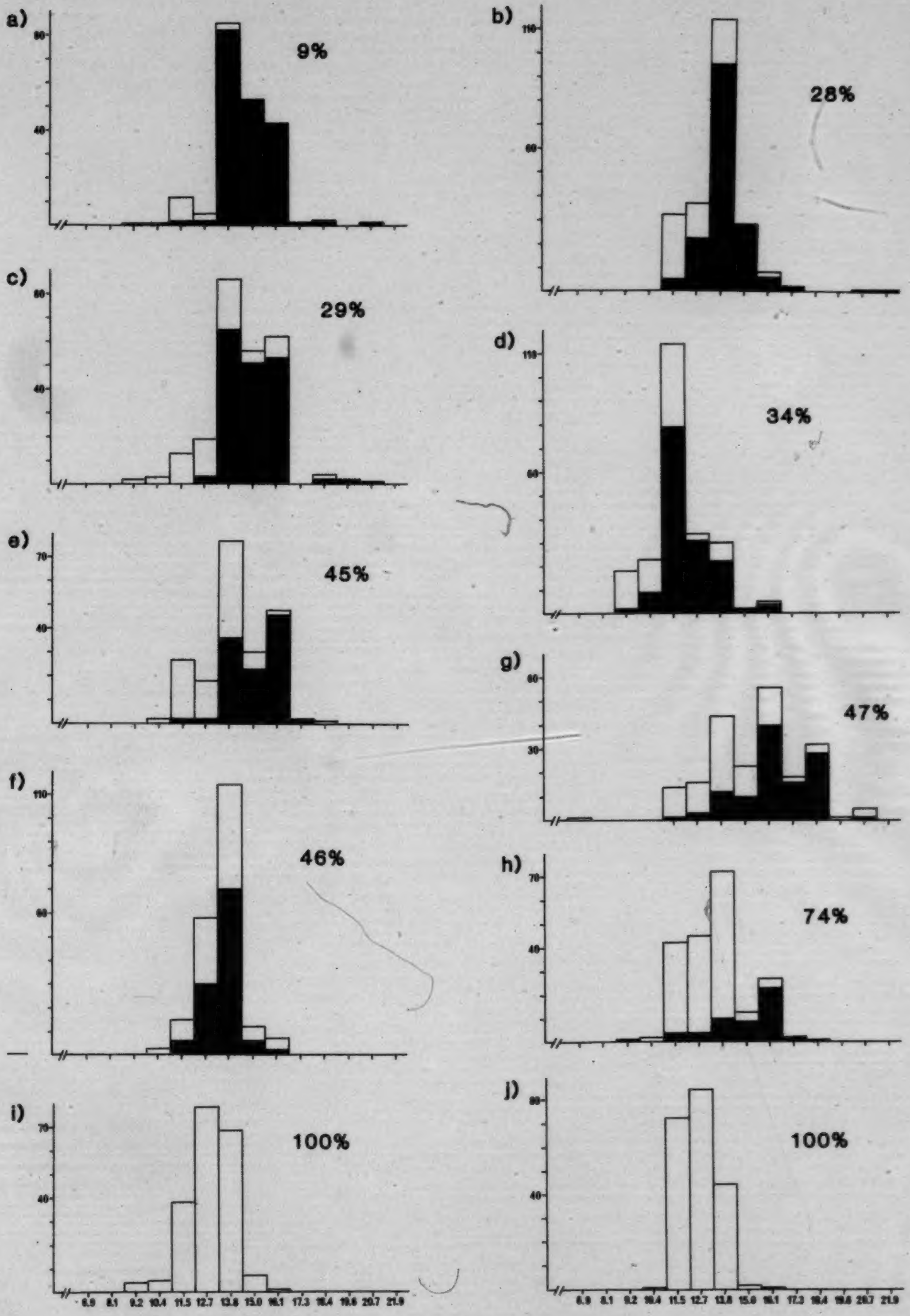
The spores from these ten capsules were mounted on a glass slide (vouchers in ALTA) in Hoyer's Solution and approximately 200 from each capsule were randomly selected. The diameter of each spore was measured in the longest dimension and each was scored as either plus or minus depending on whether they were turgid or collapsed. Coloration was also noted (either brown or green). The size frequencies and condition (turgid versus collapsed) of the spores in each capsule are represented in Fig. 94. Mogensen (1978a, 1978b) has 2 stressed that smaller and larger spores do not disperse randomly in a liquid medium on a slide, and that this factor must be taken into account when selecting spores for measurement. While it may be true in theory that the smaller spores will travel farther out from the centre of the slide than the larger spores, I have seen little evidence supportive of this statement, particularly when the liquid medium is Hoyer's Solution. Furthermore, calculations based upon the method of analysis suggested by Mogensen (1978b) to compensate for non-random dispersal suggest that this method may actually lead to distortion of the relative proportions of small and large spores. Therefore this methodology was not employed in the present study.

In order to test the viability of these spores of Bryobrittonia, the spores from one capsule (Horton 14481) were placed in a petri dish on filter paper moistened with distilled water. This dish was maintained under conditions of 10 hours of light (flourescent) and 14 hours of darkness at 20°C until germination tubes were present on a significant proportion of the spores (four days).

A further test for viability, the T.T.C. (Tri-phenyl Tetrazolium Chloride) test for dehydrogenase activity was also carried out. The spores from one capsule (Horton

Figure 94. Bryobrittonia longipes. Intra- and Interpopulational Variation in Spore Structure.

The percentage of spores in each capsule that are collapsed and appear to be dead is indicated.


a)
80
40
9%
b)
110
60
28%
c)
80
40
29%
d)
110
60
34%
e)
70
40
45%
f)
110
60
46%
g)
60
30
47%
h)
70
40
74%
i)
70
40
100%
j)
80
40
100%
6.9
8.1
9.2
10.4
11.5
12.7
13.8
15.0
16.1
17.3
18.4
19.6
20.7
21.9

14482 ALTA; this collection is from the same population of Bryobrittonia as Horton 14481) were stained with T.T.C. and the staining properties of the different spore types (turgid versus collapsed and brown versus green) were noted.

The analyses indicate the following irregularities in spores of Bryobrittonia. Firstly, the range of variation in size that generally occurs within a single capsule is almost as great as that known to occur in all populations of this species, that is, from nine to 18 microns (Fig. 94). This is unusual by comparison to most species of Encalyptaceae where the range of variation within a single capsule or population generally does not vary more than four or six microns. (However, there are other exceptions. For example, intrapopulational spore size is similarly more variable in one population of E. brevipes (see discussion of Variation of E. brevipes)). Furthermore, there are two types of spores in capsules of Bryobrittonia; those that are turgid and chlorophyllose, and others that are more-or-less collapsed (Fig. 87), some of which are brown and appear devoid of contents. The collapsed spores tend to be those that are smaller, but there are also large spores that are collapsed and brown. The proportion of collapsed versus turgid spores is highly variable between and even within popuations. In the ten capsules studied anywhere from nine to 100% of the spore mass consisted of collapsed spores (Fig. 94). Preliminary observations indicate that intrapopulational variation in spore size, and the occurrence of collapsed and turgid spores are also characteristic of at least some populations of E. streptocarpa (see Figs. 99, 102–103). In Bryobrittonia, there are also irregularities in the formation of spore tetrads. There are sporadic instances where cell wall formation is incomplete and two spores remain more-or-less joined, although the protoplasts are separate. Mogensen (1978a) reported this same phenomenon to occur in Cinclidium.

The results of the two viability tests are somewhat ambiguous. In the germination test only the larger spores (15–17 microns) had formed germination tubes after four days. Neither the small, collapsed spores nor the small, turgid spores had germinated. Therefore, it may be cautiously suggested that small, collapsed and brown spores of Bryobrittonia might be dead and that the small, turgid and green spores are perhaps dying. Lack of synchrony in death of spores might explain the variation in proportions of dead spores, noted above, if the capsules sampled were of different ages (which they undoubtedly were, at least in some instances).

The T.T.C. test for viability was similarly inconclusive, but also suggests that the small, collapsed and brown spores are dead. None of these spores stained red (red coloration indicates a positive reaction). However, some of the larger, turgid spores turned red, but others did not. As well, some of the larger, partially collapsed spores did turn red. In contrast, the results of a control run on spores of *Funaria hygrometrica* Hedw. obtained from a population living in the greenhouse were positive. All of the spores were turgid and chlorophyllose to begin with and all turned red with the application of T.T.C. In conclusion, it can only be tentatively suggested that the collapsed condition of some spores of *Bryobrittonia* may indicate that such spores are dead or dying.

Mogensen (1978a) reported spore mortalities of close to 50% to be characteristic of populations of *Cinclidium arcticum* (B.S.G.) Schimp. and *C. stygium* Sw. This report was based on an analysis of the staining properties of the spores; those that did not stain with acetocarmine or acetoorcein were assumed to be dead, while those that did were thought to be alive. He found that the spores that were "dead" were all smaller than the "living" spores, and that they were brownish and strongly wrinkled in contrast to the green, spherical living spores. Mogensen coined the term false anisospory for this condition and suggested that a genetically determined lethal factor would account for the death of a constant proportion of the spore mass at a particular point in spore development (this being the stationary phase, which is prior to the swollen phase that marks vegetative growth of the spores (Mogensen 1978a)). In the same study, Mogensen (1978a) also reported an 11% spore mortality in *C. subrotundum* Lindb. However, it was thought that this occurrence in *C. subrotundum* might reflect irregularities in meiotic chromosomes, which had been previously reported.

Mogensen (1978b) also reported the phenomenon of false anisospory to occur in *Macromitrium incurvum* (Lindb.) Mitt., *Rhizomnium magnifolium* (Horik.) Kop. and *Fissidens cristatus* Wils. *ex* Mitt. , with approximately 50% of the spore mass being aborted in these species, but he noted that *R. punctatum* (Hedw.) Kop. subsp. *punctatum* is isosporous and all spores are living. He described the spore mass of *R. magnifolium* and of *F. cristatus* as green and that of *R. punctatum* subsp. *punctatum* as brown, but did not characterize that of *M. incurvum*. Neither color nor structural differences (aside from size and staining qualities) were indicated for the "dead" spores of those species reported to be falsely anisosporous. It is also unclear from the study of Cinclidium (Mogensen 1978a) how many sporangia and populations were sampled, although the subsequent report of false anisospory in other genera was based on an analysis of the contents of a single sporangium of each taxon. Mogensen (1978a, 1978b) characterized false anisospory by the mature spore mass consisting of large, living and green spores mixed with small, dead and brown spores. He also emphasized that false anisospory is a constant feature of populations in all three species of Cinclidium and concluded that this condition therefore has relevance in taxonomic considerations of these species. In Bryobrittonia there are larger, green spores and smaller spores, some of which are brown and collapsed, which therefore may be interpreted as being dead; however, there are also larger spores that are collapsed and brown, and small spores that are turgid and green. Therefore, the relative size frequencies of the "dead" and "living" spores of Bryobrittonia do not conform to the bimodal distribution prescribed by Mogensen for false anisospory. Also, it appears that there is neither interpopulational constancy nor intrapopulational predictability of the relative proportions of "dead" and "living" spores that occur in capsules of Bryobrittonia. Therefore, the irregularities in spores of Bryobrittonia are not a reliable taxonomic criterion, and data based upon observations of a single capsule or population of any species of moss should be interpreted with caution. Also, there is a need to refine techniques and define reliable criteria for determining viability of spores.

The model of a genetically determined lethal factor proposed by Mogensen (1978a) to account for the 50% mortality and false anisospory in spores of Cinclidium arcticum and C. stygium cannot account for the variable mortality rates observed in Bryobrittonia. Chromosome numbers of n=13, 26 (Inoue 1974) and 52 (Lazarenko 1967) have been reported for populations of Bryobrittonia. Therefore, it is possible that chromosomal irregularities at meiosis associated with the polyploidy might account for the irregularities observed in the spores, as Mogensen (1978a) suggested for Cinclidium subrotundum.

Phylogenetic Relationships: The following features in common indicate that Bryobrittonia is most closely related to E. streptocarpa and E. procera: the long, double peristome with the teeth opposite and more-or-less fused to the segments; the furrowed capsule with a narrow, poorly differentiated rim; the well-developed, deciduous annulus; the small apolar spores that are green and finely scabrate or scabrate-rugulate; the relatively large, opaque calyptra with the rostrum ill-defined and the base of the cylinder erose or irregularly attenuated; and the long seta that is tapered distally. As well, Bryobrittonia and E. streptocarpa are the only species in the Encalyptaceae that are dioicous.

Specimens Examined: ALA (25), ALTA (85), CANM (25), E (1), H-Br (1), Priv. Herb. D. G. Horton (25), MO (2), NY (100), S (4), UAC (3), UBC (8).

ENCALYPTA Hedwig

Spec. Musc. 60. 1801.

Leersia Hedw. ex Batsch, Tab. Afd. 264. 1802. Hom. illeg. incl. gen. prior.

Plants to 50 mm tall, color as for family, ± branched, otherwise as for family. Stem in transverse section with epidermal cell walls orange to dark-orange, cortical cell walls yellow to orange, dark-orange in few, central strand undifferentiated or indistinct in most, when present walls hyaline to (in few) yellow, otherwise as for family. Brood bodies absent or (in E. streptocarpa and E. procera) present, as for family. Axillary hairs sparse or (in E. affinis) abundant, as for family. Leaves with laminae inflexed to conduplicate or (in E. mutica) plane, oblong to ligulate, lingulate, elliptic-oblong, obovate-oblong, ovate-oblong or ovate-lanceolate, otherwise as for family; margins entire, otherwise as for family. Costa with adaxial surface papillose with laminal-type cells above; in transverse section 2-4 rows of ventral cells, begleiters undifferentiated in most, 2-8 rows of abaxial stereids, abaxial epidermal cells undifferentiated or 1-2 rows with lumina slightly enlarged, walls strongly thickened, otherwise as for family. Upper laminal cells 7-18(20) µm long, walls papillose in transverse section papillae consist of short, digitate clusters of basally hollow wall outgrowths, otherwise as for family; upper *marginal cells* with lumina ovate, walls strongly thickened marginally, otherwise as for family; *transitional cells* with walls on adaxial surface smooth well above basal cells or papillae extend almost to basal cells, papillae ± as on upper cells, on abaxial surface smooth well above basal cells or papillae extend to basal cells, papillae ± as on upper cells or enlarged, some ± "o"-shaped, much-branched, branches longer than on upper cells, papillae extend farther basipetally on abaxial than on adaxial surface; *basal laminal cells* 14–120 μm long, (7)12–23 μm wide, ± distinctly differentiated with transverse walls ± strongly thickened particularly at corners, orange to dark-orange, yellow in few, entire or perforated by 1 large pore, longitudinal walls thin, hyaline to orange, entire or perforated by 1 large pore, walls thin, hyaline to orange, smooth or (in *E. affinis*) papillose abaxially, irregularly perforated; otherwise as for family; *basal marginal cells* undifferentiated to ± distinctly differentiated in 2–20 rows, otherwise as for family. Goniautoicous or (in *E. streptocarpa*) dioicous. *Perichaetial leaves* ± differentiated by ± broad, sheath-like base, basal laminal cells less distinctly differentiated in many, otherwise ± as vegetative leaves; *perigonial leaves* distinctly differentiated, 0.8–1.2(1.5) mm long, broad and sheath-like; *perigonial paraphyses* with cells uniform in size, otherwise as for family.

Seta 2–20 mm long, otherwise as for family. *Capsule* with neck indistinct or (in *E. affinis* and *E. longicolla*) ± well-differentiated, otherwise as for family; *exothecial cells* and *rim cells* as for family; *stomata* superficial to (in *E. streptocarpa*) superficial or indistinctly immersed, otherwise as for family. *Peristome* and *operculum* as for family. *Annulus* undifferentiated in most or (in *E. streptocarpa* and *E. procera*) prominent, as for family. *Spores* and *calyptra* as for family. *Chromosome number* n=13 or 26 in most, fewer with n=12, 14, 27 or 39.

Type: *Encalypta ciliata* Hedwig.

Nomenclatural Notes: Coker (1918) cited Schreber (1791) as the original author of the genus *Encalypta* and designated "*Bryum extinctorium* L." as the type species. While Hedwig (1801) included *Bryum extinctorium* as a synonym of *E. vulgaris* in Species Muscorum, Coker's selection can be regarded as arbitrary. It is apparent that she was not considering the species included in the genus by the original author. Three species presently considered as encalyptas, *E. vulgaris*, *E. ciliata* and *E. streptocarpa*, were described by Hedwig (1801). However, his circumscription of the genus *Encalypta* on the basis of a simple peristome of 16, narrow teeth, and perigonia that are bud-like and lateral excludes *E. streptocarpa* from consideration as a potential generitype. With respect to the other two species, *E. vulgaris* is characterized by the lack of a peristome although some populations with a fragile, vestigial peristome do occur, while *E. ciliata* is typified by the character-states included in the protologue by Hedwig. Coker's type of *Bryum extinctorium* is rejected on the grounds that the choice was an arbitrary one (Article 8, ICBN) and because the species does not clearly accord with the original description of the genus in Hedwig (1801) as does another species treated in this same work (Article 7.12). Therefore, *E. ciliata* is chosen here as the type species of *Encalypta*.

KEY TO SPECIES OF ENCALYPTA

1a. Spores heteropolar with sculpture of proximal and distal surfaces markedly differentiated (Figs. 68-69), proximal surface with narrow radial plicae, granular or ± smooth to rugulate centrally, trilete mark undifferentiated to ± well-defined (Figs. 200-204, 239, 256), distal surface either with prominent, warty or vermiform protuberances (Figs. 70, 238) or with ± prominent central pit bordered by ± prominent rim and 5-7 radial ridges, pit, rim and ridges ± smooth to ± rugulate (Figs. 194-199, 205-210); peristome present and ± well-developed to vestigial, 1 layer of teeth (endostome) with vertical division on outer surface of each tooth absent (Figs. 50-51, 61-62), teeth 0.4 mm long, dark-red to white or hyaline, or peristome absent (Fig. 52) . . . . **2.**

1b. Spores isopolar or paraisopolar with sculpture of proximal and distal surfaces undifferentiated or indistinctly differentiated (Figs. 65-67), gemmate or verrucate with prominent, warty protuberances (Figs. 140-148, 161-171); peristome present and well-developed, 2 ± fused layers of teeth (exostome and endostome) with vertical division on outer surface of each tooth (Figs. 47-49, 54, 58-59), teeth

0.4–1.2 mm long, dark-red to white, or peristome absent . . . . **13.**

2a. Spores on distal surface with prominent, warty or vermiform protuberances, trilete mark undifferentiated or ill-defined (Figs. 238–241, 267–270) . . . . **3.** (**E. rhaptocarpa–E. vulgaris** Complex).

2b. Spores on distal surface with ± prominent central pit bordered by ± prominent rim and 5–7 radial ridges, pit, rim and ridges ± smooth to ± rugulate, trilete mark well-defined (Figs. 196–213) . . . . **11.** (**E. ciliata** and Closely Related Taxa).

3a. Spores with elongate, vermiform protuberances on distal surface, warty protuberances few or absent (Figs. 267–270); peristome absent; leaves muticous . . . . **E. flowersiana** (p. 341).

3b. Spores with warty protuberances on distal surface (Figs. 238–241); peristome present and ± well-developed to absent; leaves muticous, apiculate or hair-pointed . . . . **4.**

4a. Leaves with abaxial surface of costa in upper half covered with long (100–165 μm), dense spines (Fig. 13); leaves muticous; peristome absent to vestigial; calyptra rostrum ≤1.2 mm long . . . . **E. armata** (p. 375).

4b. Leaves with abaxial surface of costa in upper half with shorter (46–80 μm), sparse projections, or with low, rounded scindulae or low and branched papillae, or smooth (Figs. 11–12); leaves muticous, apiculate or hair-pointed; peristome absent to ± well-developed; calyptra rostrum 0.5–2.0 mm long . . . . **5.** (also, see Table 4).

5a. Peristome present and ± well-developed; capsule ± deeply, longitudinally furrowed with dark-red ribs (ribs faint in some young capsules); leaves hair-pointed, inconspicuously keeled in upper part on abaxial surface by green, ± shiny costa; basal laminal cells prominent with dark-red or orange walls . . . . **6.**

5b. Peristome absent to vestigial; capsule ± smooth to lightly furrowed with ribs undifferentiated to pale-orange; leaves muticous, apiculate or hair-pointed, prominently keeled in upper part on abaxial surface by golden- to dark-brown, shiny costa to inconspicuously keeled by green, ± shiny to dull costa; basal laminal cells ± inconspicuous with yellowish to pale-orange walls . . . . **7.**

6a. Base of calyptra entire to erose . . . . **E. rhaptocarpa s. str.** (p. 304).

6b. Base of calyptra fringed, segments lanceolate-truncate and well-defined . . . . **E. vittiana** (p. 315).

7a. Leaves hair-pointed, hair-point hyaline, leaves ± inconspicuously keeled in upper part on abaxial surface by green to brown, ± shiny to dull costa . . . . **8.**

7b. Leaves muticous or stoutly apiculate, leaves ± prominently keeled in upper part on abaxial surface by golden to dark-brown, shiny costa to ± inconspicuously keeled by green, dull costa . . . . **9.**

8a. Calyptra pale-golden and almost transparent with capsule details discernible through calyptra; base of calyptra fringed, segments ± well-defined . . . . **E. spathulata s. str.** (p. 324).

8b. Calyptra golden to brown distally and transluscent with capsule barely visible through calyptra; base of calyptra entire . . . . **E. intermedia** (p. 353) (few North American populations).

9a. Calyptra with base of cylinder entire to erose . . . . **10.**

9b. Calyptra with base of cylinder constricted and fringed, segments linear and ± well-defined . . . . **E. asperifolia** (p. 362).

10a. Capsule ± furrowed, ribs indistinct to orange; seta 1–4 mm long; leaves inconspicuously keeled in upper part on abaxial surface by green, dull costa; calyptra rostrum 0.8–1.0 mm long, base of cylinder reaches or very nearly reaches uppermost leaves . . . . **E. intermedia** (p. 353) (most North American populations).

10b. Capsule ± smooth, ribs undifferentiated; seta 4–8 mm long; leaves prominently keeled in upper part on abaxial surface by golden to dark-brown costa; calyptra rostrum 1–2 mm long, base of cylinder is raised well above uppermost leaves . . . . **E. vulgaris s. str.** (p. 359).

11a. Leaves with margins plane; apex muticous; peristome absent to vestigial . . . . **E. microstoma** (p. 285).

11b. Leaves with margins narrowly to broadly recurved in mid-portion distally from basal cells, apex mucronate to apiculate or muticous; peristome well-developed to absent . . . . **12.**

12a. Calyptra smooth to sparsely papillose distally; peristome well-developed to absent; leaves mucronate to muticous or stoutly apiculate . . . . **E. ciliata** (p. 249).

12b. Calyptra densely papillose throughout; peristome absent; leaves hair-pointed to muticous . . . . **E. sibirica** (p. 282).

13a. Vegetative portion of plants with ± prominent clusters of brown, filamentous brood bodies in leaf axils (Figs. 3, 97) . . . . **14. (E. streptocarpa** and **E. procera).**

13b. Vegetative portion of plants lack brown, filamentous brood bodies . . . . **18.**

14a. Some plants with sporophytes and/or emergent calyptrae . . . . **15.**

14b. All plants sterile . . . . **16.**

15a. Uppermost leaves muticous; calyptra with rostrum hardly contracted from cylinder (Fig. 71) . . . . **E. streptocarpa** (p. 118).

15b. Uppermost leaves hair-pointed; calyptra with rostrum slightly and distinctly contracted from cylinder (Fig. 77) . . . . **E. procera** (p. 128).

16a. Population found in North America or Asia (east of the Ural Mountains) . . . . **E. procera** (p. 128).

16b. Population found in Europe (west of the Ural Mountains) . . . . **17.**

17a. Population found in Scandinavia . . . . **E. streptocarpa** (p. 118) or **E.procera**.

17b. Population found in British Isles or continental Europe . . . . **E. streptocarpa**.

18a. Leaves with papillae on abaxial surface of basal cells, particularly marginally; adaxial surface smooth (Figs. 30–31, 152) . . . . **19.**

18b. Leaves with abaxial surface of basal cells smooth (some uppermost cells sparsely papillose) (Fig. 28); adaxial surface smooth . . . . **20.**

19a. Leaves muticous to broadly mucronate; costa ends well below apex to subpercurrent . . . . **E. affinis** subsp. **macounii** (p. 202).

19b. Leaves apiculate to short hair-pointed; costa excurrent . . . . **E. affinis** subsp. **affinis** (p. 201).

20a. Peristome present and well-developed, 2 fused layers of teeth with vertical division on outer surface of each tooth (Figs. 48–49, 58–59) . . . . **21.**

20b. Peristome absent . . . . **22.**

21a. Peristome teeth crimson-red; capsule with well-differentiated neck ± equal to urn in length (Fig. 46); spores 55–80 μm . . . . **E. longicolla** (p. 139).

21b. Peristome teeth white to peach-colored; capsule with neck undifferentiated or ill-defined and considerably shorter than urn (Fig. 161); spores 30–45 μm . . . . **E. brevicolla** (p. 212).

22a. Leaves with long hair-points; spores with rugulate sculpture . . . . **E. brevipes** (p. 233).

22b. Leaves muticous or apiculate; spores gemmate . . . . **23.**

23a. Leaves tapered to narrowly acute apex; stoutly apiculate, apiculus yellow; calyptra golden to golden-brown, dark-brown distally, strikingly shiny, base of cylinder lacks constriction, lacerate . . . . **E. alpina** (p. 153).

23b. Leaves oblong with the apex obtuse; muticous; calyptra pale-golden to golden-brown distally, moderately shiny to ± dull, base of cylinder ± constricted and fringed . . . . **E. mutica** (p. 168).

ENCALYPTA STREPTOCARPA Hedwig,

Spec. Musc. 62, pl. 10, figs. 10–15. 1801.
Figs. 3–4, 26–27, 35, 38, 53–54, 95–103.

Types: "Habitat in muris vetustis, fissuris rupium Helvetiae, Sudetum Silesiae, (calcarearum Franconiae, Austriae,) frequens circa Clagenfurthum Carinthaie." (Lectotype: "Encalypta *streptocarpa* Spec. Musc. p. 62 + 10. f. 10–15 Specimina Carinthiae ad Klagenfurt Silesiae in Sudetit lecta et muris vetustis Lusatiae" G-Hedw.-Schwaegr.!).

Leersia streptocarpa (Hedw.) Brid., J. f. Bot. 1800(2): 275. 1801. *Nom. Inval.*

Encalypta contorta Hoppe *ex* Lindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 20: 396. 1863. *Nom. illeg. incl. spec. prior.*

Encalypta contorta var. *adpressa* Schiffn., Sitzungsber. Deutsch. Naturwiss.-Med. Vereins Böhmen "Lotos" Prag, 46: 163. 1898. Types: "Am Mauerwerk unter der Stiftsapotheke in Hohenfurth 560 *m.* sehr reichlich; steril. -- Am Gemauer der Ruine Wittinghausen bei St. Thoma 1030 *m.* reichlich; ster. 1)... 1) Ich besitze diese Form aus dem Wusnitzthale bei Neuhutten sudlich von Prag, wo sie gemeinsam mit der Normalform vorkommt." (Lectotype: "Encalypta contorta (Wulf.) Lindb. var. adpressa Schffn. n. var. Am Gemauer der Ruine Wittinghaüsen bei St. Thoma. ± 1030 m 6/9 1896. lgt. et det. Schiffner." FH-Schiffn.!; Syntype: FH-Schiffn.!).

Encalypta streptocarpa var. *adpressa* (Schiffn.) Podp., Consp. 164. 1954.

Nomenclatural Notes: There are a number of specimens of *E. streptocarpa* in the Hedwig-Schwaegrichen herbarium and Hedwig's handwriting is on several of these. However, only one of these includes a direct reference to the description in Species Muscorum (Hedwig 1801), as well as locality information from the original description. Furthermore, two of the plants on this sheet match those illustrated by Hedwig when he described *E. streptocarpa*. Other instances where the specimen illustrated by Hedwig is still extant in his herbarium have been reported by Peterson (1977) and Koponen (1979), among others.

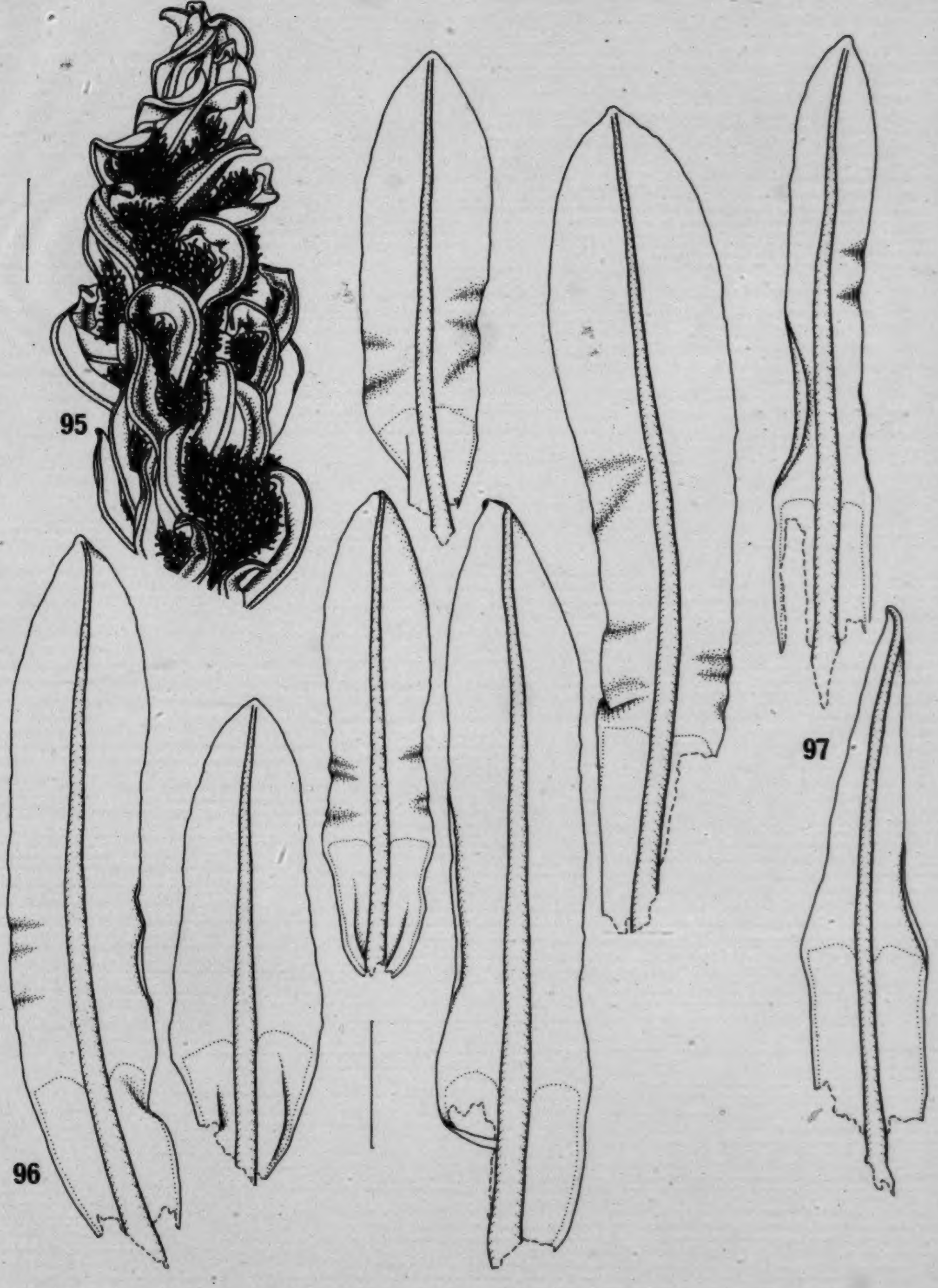
Diagnosis and Differentiation: Plants of *E. streptocarpa* are, in many populations and particularly those with sporophytes, larger than those of any other species of Encalypta A definitive feature of sterile plants is the occurrence of large clusters of brown, filamentous brood bodies in the leaf axils. Also characteristic of E. streptocarpa is the shape of the calyptra. It is so gradually tapered distally that the rostrum is virtually undifferentiated. The base of the long, narrow cylinder is either erose or it is lacerate and elongated into broad, undulate segments that give it a rather untidy appearance The calyptra is always dark golden-brown and opaque, but it is also somewhat shiny. The long peristome consists of two, unfused layers that are both erect. The orange, narrowly linear exostome teeth are positioned opposite the yellow endostome segments that arise from a well-developed basal membrane. Capsules are long-cylindric with a slight constriction just below the mouth and deeply, spirally furrowed. They are golden with the ridges more opaque than the furrows and there is a very narrow, indistinct, red rim at the mouth. The seta is generally quite long and red or orange. The long, narrow leaves with more-or-less recurved margins are always contorted and in some populations they are uniformly spirally twisted. The prominent costa is thick, golden-brown to red-brown and shiny in the upper part. It extends almost to the apex of the leaves and ends there rather abruptly. A prominent microscopic feature of the leaves of E. streptocarpa is the basal marginal border. This consists of a number of rows of very narrow cells that have yellowish walls. The transverse walls of the outer row are slightly oblique in the upper part and the margin is here very slightly crenulate with the projecting outer corners. This marginal border is distinct in most populations of E. streptocarpa; however, in some populations of sterile plants, it is poorly differentiated in the lower part and here consists of cells that are orange in color and broader, more like the basal cells. The walls on the abaxial surface of the transitional cells are papillose throughout, so the basal cells appear abruptly differentiated. The basal cells form a large and distinct group with orange transverse walls and yellow longitudinal walls. Many of the basal cells on an individual leaf of E. streptocarpa are short-oblong and the overall impression is of short, broad cells. The spores are the smallest of any species of Encalypta, green and isopolar. The minute scabrae are barely visible with the light microscope, but with the aid of SEM they appear as small, rounded, granular thickenings that are more-or-less irregularly scattered or lined up in rows such that the surface pattern is similar to that of a fingerprint, as

Figures 95-97. **Encalypta streptocarpa**. Scale=1 mm.

Fig. 95. Habit of sterile plant with brood bodies.

Fig. 96. Vegetative leaves.

Fig. 97. Perichaetial leaves.



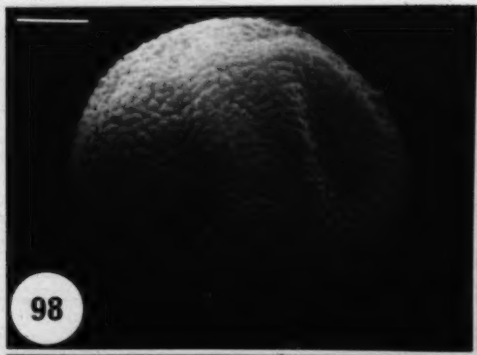
Figures 98-103. Variation in Spores of Encalypta streptocarpa.

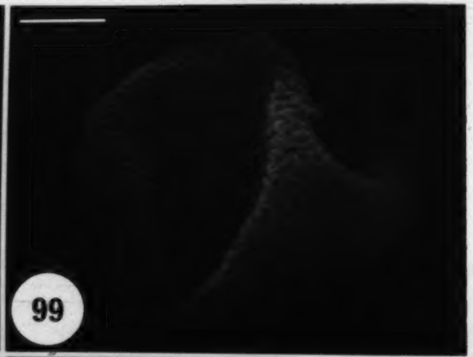
Figs. 98–99. Scale=2 μm.

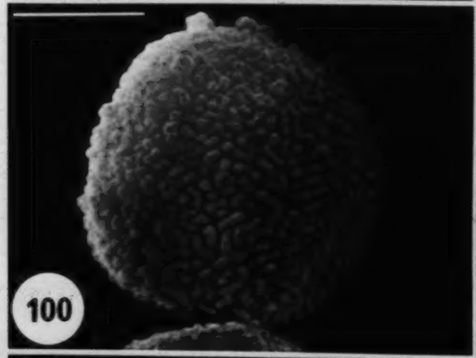
Figs. 100–101. Scale=4 μm.

Fig. 102. Scale=2 μm.

Fig. 103. Scale=4 μm.


98


99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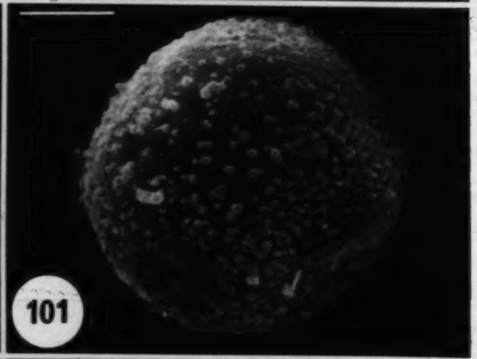
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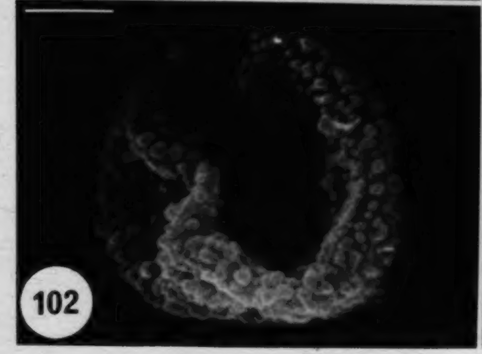
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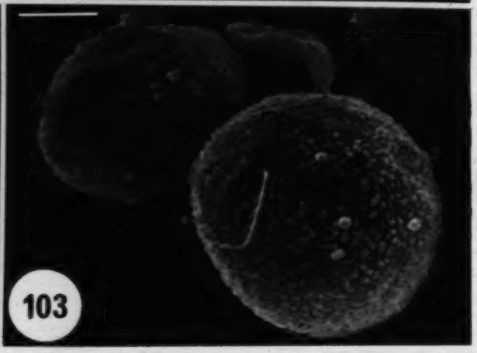

103

suggested by Járai-Komlódi and Orbán (1975).

Encalypta streptocarpa is most likely to be confused with *E. procera*. The prominent clusters of brood bodies that occur among the leaves on sterile plants of *E. streptocarpa* immediately differentiate it from all other species of *Encalypta* with which it might be confused, except *E. procera*. Differentiation of sterile populations of *E. procera* and *E. streptocarpa* is discussed under *E. procera*. Plants of *E. streptocarpa* with sporophytes are quite different than fruiting plants of *E. procera*. *Encalypta procera* is autoicous, and there are small, bud-like perigonia along the stem below the perichaetium. While the peristome of *E. procera* is very long, like that of *E. streptocarpa*, the exostome teeth and the endostome segments are more-or-less fused in the lower two-thirds, but in the upper part they are separate and the exostome teeth are strongly recurved away from the erect endostome segments. The seta is always dark-red in *E. procera*. At least the upper leaves have hyaline hair-points and the marginal border at the base of the leaves is either undifferentiated or indistinctly so in most populations. In transverse section, there are only four rows of stereids on the abaxial surface of the costa. Spores of *E. procera* range from 14 to 24 microns in diameter, while those of *E. streptocarpa* are nine to 16 microns.

Sterile plants of *E. streptocarpa* that lack brood bodies, or if the brood bodies are inconspicuous, could be mistaken for *E. vulgaris*. Muticous leaves with a prominent, shiny (at least in the upper part) costa that extends almost to the leaf apex are characteristic of both species. However, in *E. vulgaris* the leaf margins are invariably plane throughout.

Description: *Plants* to 50 mm tall, yellow- to olive-green above, some green to dark-green, some encrusted with calcareous deposit, brown to blackened below, ± branched. *Stem* in transverse section with central strand present, cells small, walls thin, or indistinct to undifferentiated. *Brood bodies* in ± dense clusters among leaves of many sterile plants, among lower leaves of some fertile plants, many attached to base of costa, filamentous, long (≤2 mm) and profusely branched in upper part, in lower part up to 10 or 12 filaments joined by longitudinal walls, cells oblong, transverse walls slightly oblique, walls smooth and hyaline to pale-orange, branched upper portion of discrete filaments with ± quadrate cells, transverse walls perpendicular, walls slightly irregular and dark-brown at maturity, strongly thickened, 1 longitudinal wall thin in some. *Axillary hairs* sparse. *Leaves* when dry incurved and regularly or quite irregularly twisted, laminae ± conduplicate and undulate, apex cucullate; 3.0–8.0 mm long, 0.6–1.5 mm wide, oblong with some slightly narrowed in mid-portion, narrowly ovate-oblong or narrowly obovate-oblong, apex obtuse, muticous; *margins* plane, 1 or both reflexed or narrowly recurved distally just above basal cells or in few intermittently nearly to apex. *Costa* subpercurrent, ends 3–8 cells below apex, abaxial surface prominently keeled, shiny above, dull from just above basal cells basipetally, yellow, golden-brown or reddish-brown, green only in uppermost leaves, densely papillose from near base to just above transitional cells, papillae large, some "o"-shaped, much-branched, ± smooth distally, strong tooth-like projections ± prominent apically; in transverse section with 2–3 rows ventral cells, begleiters undifferentiated, 5–8 rows of stereids. *Upper laminal cells* 9–16(18) µm wide, (9)12–20 µm long, with 2–4 papillae per cell, each indistinctly "c"-shaped; *upper marginal cells* 12–20 µm wide, 9–14 µm long; *transitional cells* papillose to basal cells on abaxial surface, on adaxial surface walls smooth somewhat above basal cells; *basal laminal cells* 18–60 µm long, (9)12–16 µm wide, ± prominent, transverse walls orange, longitudinal walls yellowish, superficial walls smooth, entire to irregularly ± perforated, some populations with tangled mat of narrow (7 µm) rhizoids ± attached to basal cells; *basal marginal cells* ± distinctly differentiated in 5–8 rows, transverse walls slightly oblique to margin and protruding in upper cells of outer row. Dioicous. *Perichaetial leaves* ligulate above ovate, sheath-like base, apex strongly cucullate; *perigonial leaves* 1.6 mm long, broadly sheath-like below, quickly narrowed to narrowly acute, muticous apex; *perigonial paraphyses* with some upper cells divided longitudinally, walls smooth or with low papillae.

Seta (8)10–19 mm long, flexuose, ± twisted dextrorsely near capsule, some coiled like a spring near capsule, dull to somewhat shiny, red to dark-red or orange below, some yellowish to orange above, dark-red near capsule; in transverse section (160)200–280 µm in diameter below. *Capsule* (2.3)3.0–4.3(5.0) mm long, when dry cylindric or tapered distally from broader base, dextrorsely furrowed, slightly constricted beneath rim, slightly puckered basally and abruptly narrowed to seta, golden with the spiral ridges more opaque and shiny, very narrow indistinct red rim at mouth, when young golden-green, dextrorsely furrowed or twisted, when old ± twisted, dull-orange to greyish; exothecial cells in spiral rows, 115-170 µm long, 12-18 µm wide, in transverse section superficial and adjacent radial walls on capsule ridges thickened, superficial walls 2.5-3.0 µm thick, cell walls between ridges thin; rim cells ± differentiated in 1-4 irregular rows, (5)7-20 µm long, (2.3)5-11 µm wide, walls somewhat thickened; stomata superficial to indistinctly immersed, 14-22, restricted to capsule base, 30-41 µm long, 28-46 µm wide. Peristome ≤1.2 mm long, in 2 concentric layers, exostome teeth and endostome segments unfused, 16, opposite, exostome ± erect, longer than endostome, low basal membrane present or absent, teeth filiform, orange, ± densely papillose, outer surface with 2 vertical rows of cell plates, inner surface with prominent trabeculae; endostome erect, basal membrane well-developed, ca. 1/3 height of segments, pleated with revolute flanges on outer surface between segments, fenestrate or entire, segments filliform above, pale-orange, ± densely finely papillose, outer surface with 1 vertical row of cells plates, inner surface with 2 vertical rows of cell plates at base of membrane; preperistome absent. Operculum (1.2)1.5-1.8 mm long, narrowly conic. Annulus prominent, glossy and crimson-red, massive, ± deciduous in fragments, 3 rows of cells, outer walls thickened, opaque, inner walls thin, transluscent, when wet cells inflated radially and periclinally. Spores olive-green, circular to elliptical, isopolar, 9-16 µm, ± even in size within individual capsules to uneven with some larger and smaller spores, minutely scabrate or scabrate-rugulate. Calyptra (5)7-10(11) mm long, extends well below capsule, narrowly long-cylindric, gradually or slightly but distinctly contracted to slightly curved or erect rostrum that is (1.2)1.5-2.0 mm long, cylinder erose at base or elongated and ± lacerate, calyptra dark golden-brown in most to golden-brown, very opaque, shiny, ± papillose above, smooth below, papillae ± large and spiny, low and rounded basipetally; cells on outer surface of cylinder in slightly spiral rows; in transverse section cylinder with 4-5 rows of cells with small lumina, walls very thick. Chromosome number unreported.

Habitat: Encalypta streptocarpa is one of a few species of Encalypta that are not restricted to montane and arctic habitats. It is widespread through the lowlands, as well as the mountainous regions, of Europe. This is the species of Encalypta that characteristically forms more-or-less extensive tufts in the crevices of stone walls. Encalypta streptocarpa is also found on exposed soil on rock outcrops and in crevices of outcrops. Populations occur in both shaded and exposed habitats. Encalypta streptocarpa is generally associated with calcareous substrates. Limpricht (1890) reported it to occur "An Kalkfelsen und kalkhältigen Gesteinen..." and Nyholm (1954) noted that it occurs "...preferably in calcareous districts,...". However, I have also collected it growing in seeps over granite so I suspect that it may also have a tolerance of slightly subneutral conditions. Similarly, E. alpina is generally found in association with calcareous rocks, yet populations that were growing in seeps over granite were in soil with a slightly subneutral pH, not as acidic as one might expect considering the nature of the substrate (see Habitat of E. alpina). Therefore, an acidic substrate does not necessarily mean that the conditions will be strongly acidic.

Distribution: Encalypta streptocarpa can be differentiated from E. procera with certainty only on the basis of plants with sporophytes (see Diagnosis and Differentiation of E. procera). As such plants are presently known only from Europe, it is assumed that E. streptocarpa is endemic to this region. I have examined fruiting specimens from Scandinavia, Great Britain, Poland, East Germany, Czechoslovakia, West Germany, Netherlands, Belgium, France, Spain, Switzerland, Italy, Austria, Hungary, Jugoslavia, Roumania, Turkey and Iran.

The range of E. streptocarpa, which includes the hotter, drier Mediterranean regions, extends farther south than that of most species of Encalypta, except for some taxa in the E. rhaptocarpa-E. vulgaris complex and E. ciliata. Encalypta streptocarpa is ubiquitous throughout Europe, particularly in the sterile form. Sterile populations are generally extensive, as are the fruiting populations, judging by the number of exsiccata collections, but the latter are less common than the sterile populations.

Variation: Preliminary observations indicate that spores of E. streptocarpa, like those of Bryobrittonia (see discussion of Variation under B. longipes), are subject to considerable intrapopulational variation in size . Also, some spores are collapsed and appear dead (Figs.

99, 102–103), while others are turgid and appear to be viable (Figs. 98, 100–101, 103).

Phylogenetic Relationships: Encalypta streptocarpa is undoubtedly most closely related to E. procera. Characteristics that indicate this relationship include not only sporophytic, but also vegetative features. Both are characterized by an opaque, papillose calyptra that is long and narrow, a long-cylindric capsule that is deeply, spirally twisted, a well-developed, revoluble annulus, a conic-rostrate operculum, a long, double peristome with the opposite endostome and exostome more-or-less unfused and the endostome with a well-developed basal membrane, and a relatively long seta. The most significant vegetative characteristic that links E. streptocarpa with E. procera is the filamentous, brown brood bodies that typify sterile plants of both species. As noted in the discussion under Structure, these are the only species of Encalyptaceae with this characteristic. As noted under E. procera, many sterile populations of E. streptocarpa and E. procera are undifferentiable. However, even fertile populations have vegetative characteristics in common including papillae on the abaxial surface of the costa, transitional cells with papillae extending to the basal cells on the abaxial surface and prominently colored basal cells.

On the basis of sporophytic structures and the dioicous sexual condition, it is probable that E. streptocarpa is also closely related to B. longipes (see Phylogenetic Relationships of B. longipes).

Specimens Examined: BP (80), G (5), JE (290), PRC (95).

ENCALYPTA PROCERA Bruch,

Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 1:
283, pl. 11, figs. 1–18. 1832.
Figs. 20, 47, 104.

Type: "An felsen auf Alpen in Norwegen in dichten Rasen. (Kurr)." (Lectotype: "Encalypta procera auss Norwegen Hubner Kurr 1828" BM-Schimp.!).

Encalypta selwynii Aust., Bot. Gaz. (Crawfordsville) 2: 109. 1877. Type: "Vancouver's Island, May, 1875. Macoun." (Holotype: "No. 37 Encalypta selwyni n.sp? Vancouver. 1875 (May) Macoun" NY!).

Leersia procera (Bruch) Lindb., Musci Scand. 19. 1879. Nom. inval.

Leersia selwynii (Aust.) Britt., Bull. Torrey Bot. Club 18: 50. 1891. Nom. inval.

Encalypta cucullata C. Müll. et Kindb. in Macoun et Kindb., Cat. Canad. Pl. 6: 96. 1892. Type: "On earth along the west bank of the Columbia River, at Revelstoke, B.C., May 9th, 1890. (Macoun)" (Lectotype: "Canadian Musci 491. Encalypta cucullata, C.M. & Kindb. (N.Sp.) On earth in crevices of rocks along the Columbia River, at Revelstoke, B. C., May 9th, 1890." S-Kindb.!; Isotypes: NY (2 specimens (in part))!).

Nomenclatural Notes: There are two specimens of E. procera in the Schimper herbarium, which is one of the depositories of Bruch's herbarium cited in Sayre (1977), with label data that correspond more-or-less to those in the protologue of E. procera. One of these has "Encalypta procera nob. Kongsvold Norvegiae Dr. Kurr." written on it; the other, "Encalypta procera Aus Norwegen Hubner Kurr 1828". The plants in neither specimen appear to match the illustration that accompanies the original description. The first specimen is in poor condition and there is no date of collection to indicate that this specimen was in the author's herbarium at the time when E. procera was described. In contrast, the other specimen, which is well preserved and consists of numerous plants, clearly was collected prior to the publication of the new species. Therefore, the latter has been selected as the lectotype.

Diagnosis and Description: Characteristic of E. procera in most populations that include some sterile plants are the masses of brown, filamentous brood bodies that occur in the leaf axils. Plants of E. procera with sporophytes are defined by a combination of features. The long, narrow calyptra is tapered gradually to the rostrum or there is a slight, but distinct contraction so that the rostrum is differentiated from the cylinder. The base of the cylinder is either erose, or lacerate and elongated into long, more-or-less undulate segments. The calyptra is golden and the segments, when present, are generally whitish. The long, double peristome consists of 16 exostome teeth that are opposite 16 endostome segments. The two layers are fused in the lower two-thirds; however, in the upper part the exostome teeth are strongly recurved away from the erect endostome segments in the dry condition. The lower part of the endostome is a well-developed basal membrane. The cylindrical capsule is spirally or longitudinally furrowed, slightly constricted below the mouth and abruptly narrowed to the rather long, dark-red seta. Leaves are generally somewhat twisted on plants with sporophytes, but are almost untwisted in some sterile populations when the axillary brood bodies are particularly prolific. In E. procera, the leaves are dimorphic. The costa is subpercurrent or percurrent on leaves in sterile popuations, but is excurrent as a hyaline hair-point on at least the upper leaves of plants with sporophytes. The leaf margins are narrowly to broadly recurved shortly in the mid-portion of the leaf or almost from the apex to the leaf-base. Microscopic features of E. procera include the dark-orange or orange walls of the basal laminal cells. These extend right to the margin in some populations, but in others there is a rather ill-defined marginal border in the upper part. The papillae on the abaxial surface of the transitional cells are larger than those on the upper cells and extend to the basal cells. The abaxial surface of the costa is similarly papillose in the transitional cell area and in transverse section, there are four rows of stereids. The green spores are minutely papillose and relatively small.

Plants of E. procera with sporophytes might be confused with those of E. streptocarpa or E. affinis subsp. affinis. Calyptra and capsule shape are very similar in E. streptocarpa; however it is easily separated from E. procera by differences in the peristome, leaves and spores. The habit of the peristome in E. streptocarpa is distinct in that both the endostome and the exostome are more-or-less erect. Also, the leaves are always muticous and there is a distinct marginal border of yellowish cells at the base of the leaves. Spores of E. streptocarpa are also green, but they are half the size of those of E. procera.

Plants of E. affinis subsp. affinis resemble those of E. procera in the short hair-points of the leaves and the recurved margins. Also, the single peristome of E. affinis subsp. affinis, which is composed of several layers of cells, bears a superficial resemblance to the fused, lower portion of the peristome of E. procera when the upper, unfused part is broken off, as it frequently is once exposed. Encalypta affinis subsp.

affinis is differentiated by the smooth, unfurrowed capsules and the basal leaf cells are papillose on the abaxial surface, particularly along the margins.

Sterile plants of *E. procera*, like those of *E. streptocarpa*, generally have abundant, brown, filiform brood bodies in the axils of the leaves. While upper leaves of plants with sporophytes are hair-pointed in *E. procera*, leaves are muticous on sterile plants and therefore similar to those of *E. streptocarpa*. The taxonomic problems that arise from these structural similarities between sterile plants of *E. streptocarpa* and *E. procera* have seldom been dealt with in the literature. When Bruch (1832) described *E. procera*, it was on the basis of plants with sporophytes, but he also reported and illustrated axillary brood bodies. Limpricht (1890) only included a short mention of *E. procera* and described the more obvious differences between fruiting plants of this species and *E. streptocarpa*, but did not mention the similarities between sterile plants of the two species. A specimen in Lindberg's herbarium that contains both fruiting and sterile plants of *E. procera*, but is determined as "*Encalypta procera* c.fr. + *E. streptocarpa* sterile" gives some indication that *E. procera* probably was not well understood at that time. Later, Brotherus (1923) in Die Laubmoose Fennoskandias gave a complete treatment of both *E. procera* and *E. streptocarpa* (as *E. contorta*) and noted under *E. procera* "Vegetative Vermehrung wie bei *E. contorta*.", but he did not give any discussion and his key separates the two taxa on the basis of sporophytic character-states. Flowers (1938) was clearly aware of the problem. He stated that "I found it very difficult to separate *E. streptocarpa* and *E. procera* with muticous leaves in the sterile condition.", but Flowers concluded that a careful study of gametophytic structures had led to the discovery that there is a central strand in *E. procera*, but that this is indistinct or lacking in *E. streptocarpa*. Nyholm (1954) also considered the presence or absence of a central strand to be a 'good' taxonomic feature for differentiating between these two species. Lawton (1971) reported that *E. streptocarpa* differs from *E. procera* not only in the absence of a central strand, but also in the muticous apex of the leaves and the plane leaf margins. Crum (1973) did not place any taxonomic importance in the presence or absence of a central strand for differentiating between *E. streptocarpa* and *E. procera*.

The central strand is not always well-developed in sterile populations of *E. procera*, in my experience. Furthermore, I have not been able to discover any other character-states that consistently differentiate all sterile populations of *E. procera* from those of *E. streptocarpa*. However, one or more of the following features is useful in some instances; some populations simply cannot be identified with certainty. In *E. streptocarpa* the costa is always thick and prominent at the apex of the leaf, while in some populations of *E. procera* the costa ends well below the apex. In plants with no suggestion of a basal marginal border to the leaves, it is safe to assume that these are *E. procera*. However, in both *E. procera* and *E. streptocarpa* populations occur in which the marginal border is weakly differentiated. The basal cells in many populations of *E. procera* are dark-orange on both the longitudinal and transverse walls; such dark coloration does not occur in *E. streptocarpa*. However, in some populations of *E. procera*, the walls are paler and orange or yellow, just as they are in *E. streptocarpa*. In most populations of *E. procera*, there are some basal cells that are long-oblong in contrast to the regularly short-oblong cells that characterize *E. streptocarpa*, but such elongate cells do not occur in every population of *E. procera*. The papillae that occur on the abaxial surface of the costa and the transitional cells in *E. procera* are generally larger with many that are "o"-shaped and sparser than the lower, denser papillae that occur in *E. streptocarpa*; however, there is structural intergradation in this feature too.

Description: *Plants* to 50 mm tall, green to olive-green above, brown below, ± branched. *Stem* in transverse section with central strand present, cells small, walls thin and hyaline or pale-orange, or central strand indistinct. *Brood bodies* in ± dense clusters among leaves of many sterile plants, among lower leaves of some plants with sporophytes, many attached to base of costa, filamentous, long 3 mm) and profusely branched in upper part, in lower part up to 10 or 12 filaments joined by longitudinal walls, cells oblong, transverse walls slightly oblique, walls smooth and orange, branched upper portion of discrete filaments with ± quadrate cells, transverse walls perpendicular, walls slightly irregular and dark-brown at maturity, strongly thickened, 1 longitudinal wall thin in some. *Axillary hairs* sparse. *Leaves* when dry incurved and almost untwisted to strongly twisted, laminae plane to inflexed to conduplicate; 2.3-5.0(6.0) mm long, 0.7-1.3 mm wide, oblong or broadly oblong to narrowly obovate-oblong or narrowly ovate-oblong, few are narrowly elliptic-oblong, apex abruptly to quickly narrowed, muticous to hair-pointed (≤1.5 mm); margins narrowly to broadly recurved on 1 or both laminae ± irregularly ± from narrowing of apex almost to leaf base. Costa subpercurrent to excurrent, abaxial surface keeled, somewhat shiny above, dull from just above basal cells basipetally, green to dark-red basipetally, golden-brown above in very few, green in uppermost leaves, ± densely papillose from near base to just above transitional cells, papillae large, many "o"-shaped, ± smooth distally or with rounded tooth-like projections, particularly at apex; in transverse section with 2-3 rows of ventral cells, begleiters undifferentiated, 4 rows of stereids. Upper laminal cells 12-16(18) µm wide, (9)12-16(25) µm long, with (2)4-5(6) papillae per cells, each ± "c"-shaped; upper marginal cells 14-16(18) µm wide, 9-12(14) µm long; transitional cells strongly papillose to basal cells on abaxial surface, papillae large, some "o"-shaped, much-branched, branches long, on adaxial surface smooth somewhat above basal cells; basal laminal cells 28-90 µm long, 12-23 µm wide, prominent, transverse walls dark-orange to pale-orange, longitudinal walls dark-orange to yellowish, superficial walls smooth, entire to ± strongly, irregularly perforated; basal marginal cells undifferentiated to ± indistinctly differentiated, in 3-4 rows, in some transverse walls slightly oblique to margin and protruding in upper cells of outer row. Goniautoicous. Perichaetial leaves ovate-lanceolate to oblong from ovate, sheath-like base, apex narrowly to broadly acute, hair-pointed; perigonial leaves 0.9 mm long, broadly oblong and sheath-like below then abruptly narrowed to broadly acute apex, apical cells rather large and sharp-pointed; perigonial paraphyses with upper cells entire, walls smooth, very few with low, rounded papillae.

Seta (8)11-20 mm long, flexuose, slightly twisted sinistrorsely in mid-portion, ± twisted dextrorsely near capsule, dull to somewhat shiny, dark-red; in transverse section 230-240 µm in diameter below. Capsule 1.9-4.0 mm long, when dry cylindric and dextrorsely furrowed, slightly constricted just below mouth, slightly puckered basally and abruptly narrowed to seta, golden with ridges golden-brown, very narrow indistinct red rim at mouth, when young golden-green and longitudinally furrowed, when old ± twisted, dull-orange to greyish; exothecial cells 62-207 µm long, (9)14-23 µm wide, in spiral to longitudinal rows, in transverse section walls evenly thickened on external surface of ridges, 6 µm thick on tangential walls, 13 µm thick on radial walls, thin between ridges; rim cells ± differentiated in 1-2 irregular rows, 7-30 µm long, 12-17 µm wide, walls slightly evenly thickened; stomata superficial, restricted to capsule base, 53–70 μm long, 46–53 μm wide. Peristome ≤ 1.0 mm long, in 2 concentric layers, exostome teeth and endostome segments ± fused in lower 2/3, 16, opposite, exostome strongly recurved in upper part when dry, longer than endostome, ± joined basally by low, fenestrate membrane, teeth filiform, dark-orange below, paler distally, ± densely papillose, outer surface with 2 vertical rows of cell plates, inner surface with prominent trabeculae; endostome erect, basal membrane well-developed, ca. 1/3 height of segments, pleated with revolute flanges on outer surface between segments, entire, segments filiform above, pale-orange, ± densely finely papillose on outer surface, smooth on inner, inner surface with 2 vertical rows of cell plates at base of membrane. Operculum 1.5–1.8 mm long, narrowly conic-rostrate. Annulus prominent, glossy and crimson-red, massive, ± deciduous in fragments, 3 rows of cells, outer walls thickened, opaque, inner walls thin, transluscent, when wet cells inflated radially and periclinally. Spores olive-green, circular to elliptical, isopolar, 14–24 μm, somewhat uneven in size in each capsule, even in very few, minutely gemmate. Calyptra (4.3)5.5–8.5 mm long, extends well below capsule, narrowly long-cylindric, gradually or some slightly but distinctly contracted distally to slightly curved or erect rostrum that is 1.4–2.0 mm long, cylinder ± undulate and ± lacerate at base, erose with age, calyptra golden to golden-brown with lacerate base brown to white with age, ± opaque, shiny, ± papillose, some smooth basipetally, papillae ± large and spinous in rostrum, low and rounded basipetally; in transverse section cylinder with 4 rows of cells with small lumina, walls very thick, lacerations . Chromosome number n=27 (Steere 1954).

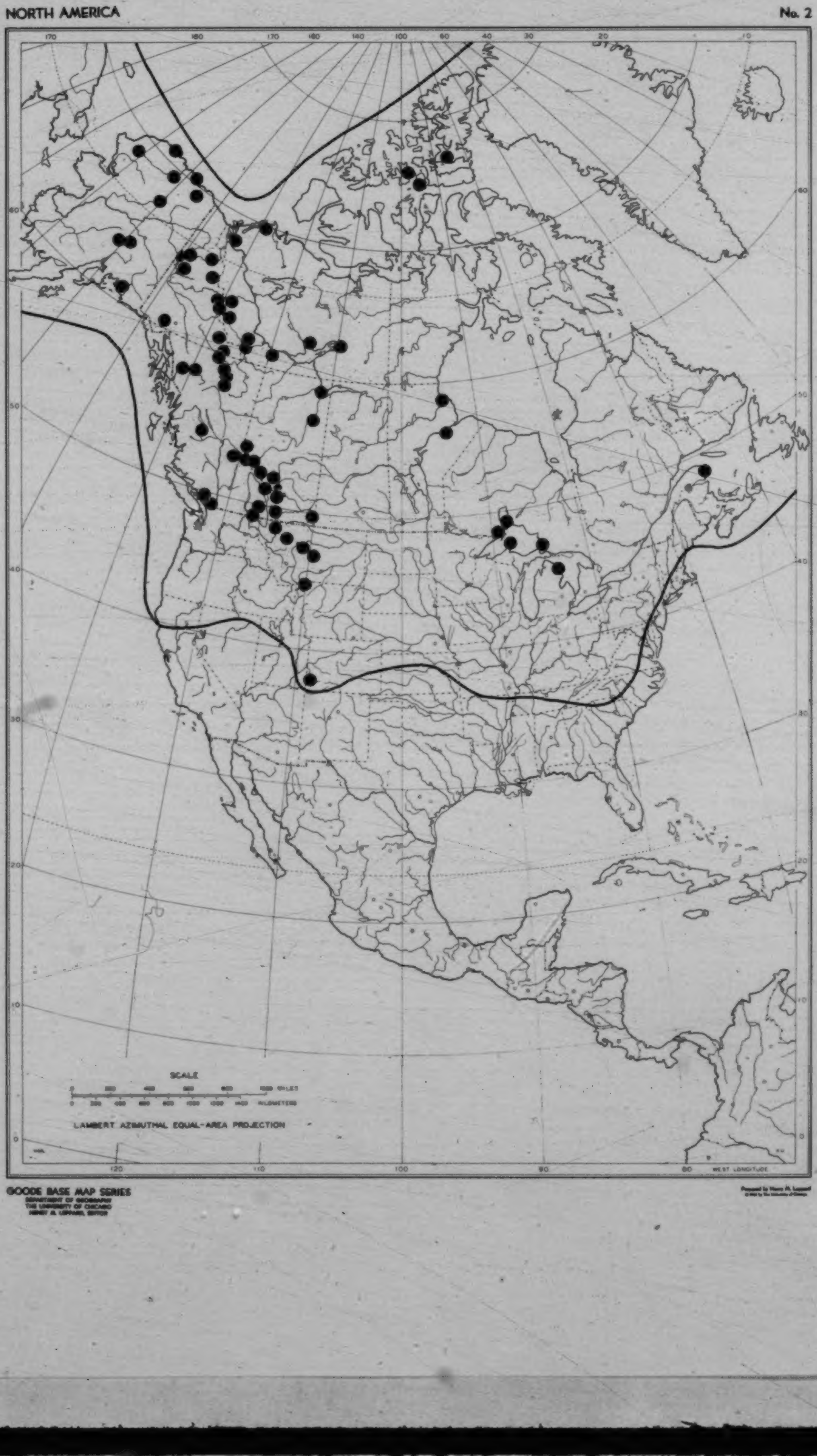
Habitat: Encalypta procera is one of a few species of Encalypta, including E. ciliata, E. rhaptocarpa and E. streptocarpa, that are not restricted to montane habitats. Populations of E. procera are also widespread in appropriate habitats, generally shaded rock outcrops, in arctic, subarctic, boreal, northerly prairie and northerly deciduous forest regions. Plants of E. procera with sporophytes characteristically grow in mesic habitats in luxuriant bryophyte mats associated with rock outcrops, or on road bank or river bank overhangs. The organic content of the soil is characteristically quite high. Two species that are consistent associates of E. procera with sporophytes are Distichium capillaceum

(Hedw.) B.S.G. and *Ditrichum flexicaule* (Schwaegr.) Hampe. Other species that are frequently found with *E. procera* are *Arnellia fennica* (Gott.) Lindb., *Campylium chrysophyllum* (Brid.) J. Lange, *Cyrtomnium hymenophylloides* (Hub.) Kop., *Eurhynchium pulchellum* (Hedw.) Jenn. and *Myurella tenerrima* (Brid.) Lindb. In contrast, sterile plants of *E. procera* are characteristically found in the crevices of rock outcrops, although they also occur on bare soil particularly along road banks, and the populations are mostly pure. Also, the organic content of the soil is quite low. *Encalypta procera* occurs in both forested and tundra habitats as *E. rhaptocarpa* does, but in tundra habitats, *E. procera* is almost always associated with rock outcrops whereas *E. rhaptocarpa* also occurs on soil.

Most populations of *E. procera* are associated with calcareous substrates as the associates listed above suggest. However, the results of soil analyses, primarily from western North America, indicate a tolerance of slightly subneutral conditions. The range of pH is from 6.5 to 7.5 (n=115 from 67 localities) with a mean of 7.3 (s.d.=±0.29) (Fig. 300).

Distribution: *Encalypta procera* is widespread in North America and is also reported from Scandinavia, central and northern Asia, and Antarctica. In North America, populations with sporophytes are reported from Alaska in the Brooks and Alaska Ranges and the Chugach Mountains; from the Yukon Territory in the Ogilvie, southern Richardson, Selwyn and St. Elias Mountains; from the Northwest Territories in the Mackenzie Mountains and in the Mackenzie Delta, south of Fort Simpson, around Great Slave Lake, and on Bathurst, Cornwallis and Ellesmere Islands; from British Columbia in the Coast, Cassiar and Rocky Mountains; from Alberta in the Rocky Mountains and in the Lake Athabasca and Fort McMurray areas, and in the Cypress Hills; from Montana in the Rocky Mountains; from Wyoming in the Rocky Mountains; from Colorado in the Rocky Mountains; from Manitoba; from Ontario and Michigan around the Great Lakes; and from Quebec in the Gaspe Peninsula (Fig. 104). However, if the assumption if made that all of the sterile North American populations are *E. procera*, as *E. streptocarpa* has not been found with sporophytes in North America, then *E. procera* is actually more widespread and of more frequent occurrence than it would appear from the distribution of populations with sporophytes. It is known as far south as California in the west; as far south as Nebraska

Figure 104. Distribution of *Encalypta procera* in North America.


NORTH AMERICA
No. 2
SCALE
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

and Missouri in the Mid-west; across through Ohio and Pennsylvania; and down along the eastern seaboard from Newfoundland to North Carolina. Farther north, the distribution of *E. procera* is probably relatively frequent and more-or-less continuous across the boreal zone, and less frequent, but still more-or-less continuous in the subarctic and arctic.

Historically, there has been some uncertainty that both *E. procera* and *E. streptocarpa* occur in North America. Coker (1918) reported both species, as did Flowers (1938) and more recently Lawton (1971). Flowers and Lawton stated that all North America specimens of *E. streptocarpa* are sterile. In contrast, Crum (1973) reported that "All records of *E. streptocarpa* Hedw. from North America are based on such sterile forms, which do, however, fruit on occasion and are indeed autoicous, proving them to be *E. procera*." and he concluded that *E. streptocarpa* does not occur in North America. His conclusion is probably correct, although it is possible that the genetic potential for producing either male or female plants has been lost from the gene pool of *E. streptocarpa* in North America and that some of the sterile populations of plants are actually *E. streptocarpa*.

Variation: Most of the Scandinavian populations of *E. procera* with sporophytes are somewhat different than the North American ones. The calyptra, capsule and seta are all shorter, and the capsule is longitudinally furrowed or only slightly spirally furrowed, while it is strongly spirally furrowed in most North American populations. However, there are occasional Scandinavian populations with the seta, capsule and calyptra longer, and the capsule distinctly twisted; therefore, the other character-states are regarded as part of the overall variation that occurs in *E. procera* and are not considered to warrant taxonomic recognition of plants with these features as a distinct entity.

Phylogenetic Relationships: *Encalypta procera* is most closely related to *E. streptocarpa* (see Phylogenetic Relationships of *E. streptocarpa*). There are some characteristics that are also suggestive of more distant relationships with *E. affinis* (see Phylogenetic Relationships of *E. affinis*).

Specimens Examined: ALTA (400), BM (1), CANM (30), COLO (2), H (5), MO (1), NY (8), O

(15), S (60).

ENCALYPTA LONGICOLLA Bruch,

Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 1:
282, pl. 10, figs. 1-15. 1832.
Figs. 46, 48, 58, 60, 105-113.

Type: "An Felsen auf den Wocheiner-Alpen, einzeln oder in kleinen Häufchen. (Müller)." (Lectotype: "Encalypta longicolla einzeln an felsen in den Vochein auf den ezerneperst (Schwarzenberg)" BM-Schimp.!).

Leersia longicolla (Bruch) Lindb., Musci Scand. 43. 1879. *Nom. inval.*

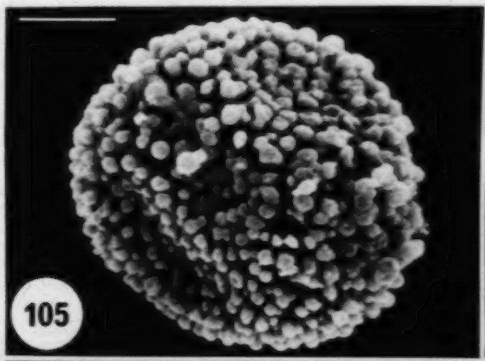
Diagnosis and Differentiation: There are several features that set *E. longicolla* quite apart from other species of *Encalypta*. The teeth of the single peristome are long and incurved in the upper part giving the whole structure the appearance of a dome. When old, the teeth do not curve inwards; they are erect and flexuose so that they stand apart, which emphasizes the broad mouth of the capsule. The shape of the capsule is unusual among species of *Encalypta*. The mouth is very broad and there is a long neck that is approximately the same length as the urn. Spores of *E. longicolla*, which are generally 70 microns in diameter, are considerably larger than those of any other species of *Encalypta*. The leaves are very narrow and sterile plants can be identified by this feature alone. Other distinctive features of *E. longicolla* include the very shiny calyptra with a distinctly defined rostrum that is short to moderately long. The base of the cylinder is lacerate-fringed. That is, the segments are narrow as they are in a distinct fringe, but there is very little, if any, differentiation of the fringe from the cylinder by a basal constriction or an inflation of the upper part of the segments. The calyptra is golden-brown and transluscent to smoky-brown and rather opaque. In many populations, the lacerate-fringed portion is white. Capsules are smooth and turgid-looking in the urn and there is a more-or-less broad constriction below the mouth, while the neck is puckered and twisted. The seta is quite variable in length, both within and between populations, but it is generally orange to reddish-black with a slight tinge of yellow in the upper part. Plants are olive-green to yellow-green, the leaves are very dense and the rather dull costa is excurrent as a long, hyaline or yellowish hair-point on most leaves. Microscopically, *E. longicolla* is characterized by clearly defined basal cells with dark-orange transverse walls that are strongly thickened. There is also a well-defined marginal border of greenish or yellowish, narrowly oblong cells. The abaxial surface of the costa is more-or-less papillose and the laminal cells extend up onto the sides of the costa so that it forms an inconspicuous keel. In transverse section, there are two to three rows of stereids in the costa. Spores of *E. longicolla* are pale brown and very irregular in shape. The urn of the capsule is so small and the spores so large that there are comparatively few in each capsule.

As noted above, *E. longicolla* is defined by several character-states that are unique within the genus *Encalypta*; therefore, there is not much likelihood of it being confused with any other species. However, the calyptra of *E. longicolla* is virtually indistinguishable from that of *E. alpina*, but *E. alpina* is distinct in the lack of a peristome, small spores and leaves that are quite broad basally, among other features. The calyptra of *E. procera* is also somewhat similar to that of *E. longicolla* in overall shape and color, but in *E. procera* it is more-or-less papillose whereas it is always smooth in *E. longicolla*. Also, *E. procera* has spirally furrowed capsules and the margins of the leaves are generally more-or-less recurved. The only other species of *Encalypta* with a capsule with a more-or-less distinct neck is *E. affinis*. However, the neck is comparatively short in *E. affinis* and the plants are considerably larger. Both *E. affinis* and *E. brevicolla* have a peristome-type that is fundamentally similar to that of *E. longicolla*. All three species have a single layer of teeth, but this is clearly the result of fusion of two layers of opposite teeth and segments, as Philibert (1889) reported. The peristome teeth of *E. longicolla* are generally longer than those of either *E. brevicolla* or *E. affinis* and they are dark crimson-red, whereas those of *E. brevicolla* are white and those of *E. affinis* are pink.

Description: *Plants* to 20 mm tall, yellow-green to olive-green and brown above, brown below, ± branched. *Stem* in transverse section with central strand indistinct. *Brood bodies* absent. *Axillary hairs* sparse. *Leaves* when dry incurved and irregularly ± twisted, laminae

Figures 105-110. Variation in Spores of Encalypta longicolla.

Fig. 105. Scale=20 μm.
Fig. 106. Scale=10 μm.
Fig. 107. Scale=20 μm.
Fig. 108. Scale=10 μm.
Fig. 109. Scale=20 μm.
Fig. 110. Scale=20 μm.



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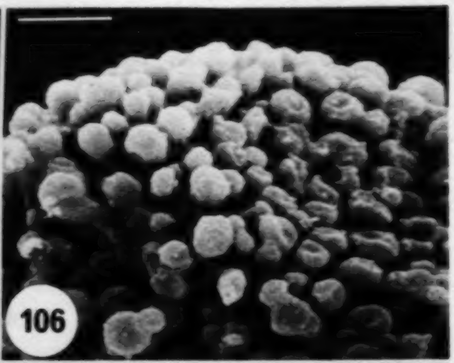

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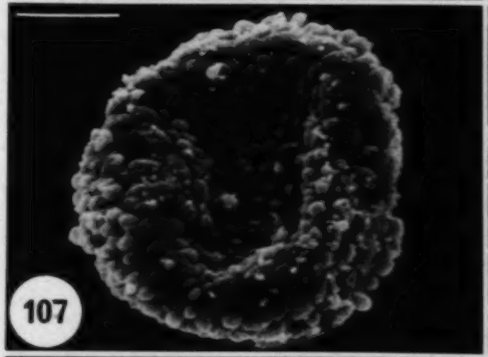

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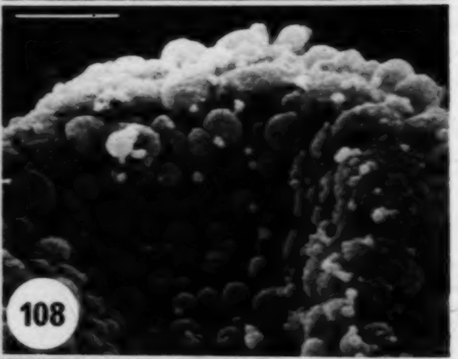

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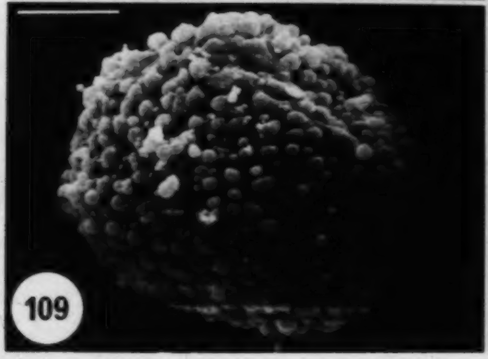

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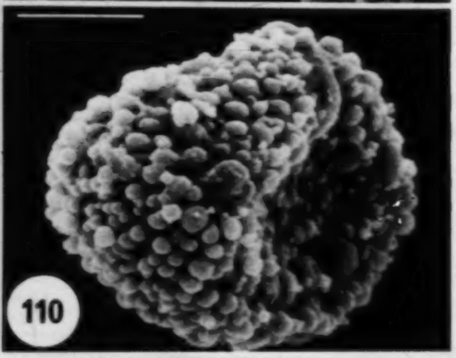


110

inflexed to conduplicate; 1.5–3.5 mm long, 0.3–0.8 mm wide, very narrowly oblong to spathulate, slightly constricted just above basal cells, quickly to abruptly narrowed to hyaline or golden hair-point that is ≤1.5 mm long, apex muticous in very few populations, brownish in many populations; *margins* plane in virtually all popuations, in very few 1 margin very narrowly and shortly recurved in the mid-portion of very few leaves. *Costa* excurrent, subpercurrent in very few populations, abaxial surface inconspicuously keeled, rather dull, green or olive-green, smooth near base, ± papillose distally, papillae low, as on upper laminal cells, laminal cells extend up sides of costa; in transverse section 3–4 rows ventral cells, begleiters undifferentiated, 2–3 rows stereids. *Upper laminal cells* 9–14(18) μm wide, 9–16 μm long, with 2–4 papillae per cell, each ± distinctly "c"-shaped; *upper marginal cells* 9–15 μm wide, 9–12 μm long; *transitional cells* strongly papillose to basal cells on abaxial surface, papillae as on upper cells, on adaxial surface smooth well above basal cells; *basal laminal cells* 14–50 μm long, 2–23 μm wide, prominent, transverse walls dark-orange, longitudinal walls yellow, superficial walls smooth, entire to irregularly ± perforated; *basal marginal cells* distinctly differentiated in 3–4 rows. Goniautoicous. *Perichaetial leaves* ± broadly oblong and sheath-like below, narrowly oblong above; *perigonial leaves* 0.7–1.3 mm long, ± broadly sheath-like below, apiculate to muticous; *perigonial paraphyses* with upper cells entire, walls smooth or with sparse, low papillae.

Seta 4–10(15) mm long, flexuose to erect, slightly twisted sinistrorsely below, ± strongly twisted dextrorsely above, shiny and orange to dark-red to dull-orange when old; in transverse section 160–185 μm in diameter. *Capsule* 1.2–2.0 mm long, when dry short-cylindric, ± broadly constricted below broad mouth, gradually contracted to seta through long, puckered and slightly twisted neck, very few abruptly narrowed to seta, smooth and ± turgid, golden, ± crimson around mouth and in neck, when old wrinkled or ± spirally striate and expanded at mouth, dull-orange; *exothecial cells* 40–120 μm long, (9)16–23 μm wide, in longitudinal rows, in transverse section walls evenly thickened on external surface, 3–5 μm thick; *rim cells* in 1–3 irregular rows, 12–14 μm wide, (3)9–16 μm long, walls somewhat thickened; *stomata* superficial, 15–17, restricted to capsule neck, 35–44 μm long, 30 μm wide. *Peristome* to 0.6 mm long, in 2 concentric layers, exostome teeth and endostome segments fused, 16 to +16, erect and strongly incurved in the upper part, lanceolate-linear, some ± divided longitudinally, crimson-red, erect and flexuose when old, exostome outer surface with 2 vertical rows of cell plates, ± densely papillose with low, rounded papillae, endostome inner surface with 2 vertical rows of cell plates, smooth to ± papillose; preperistome absent. Operculum 1.0-1.5 mm long, convex-conic, long and broadly rostrate. Annulus undifferentiated. Spores pale- brown, isopolar, rather irregular in shape with depressions, 55-80 µm, ± densely gemmate. Calyptra 3.5-6.0 mm long, extends well below capsule, long-cylindric and distinctly contracted to slightly curved or erect rostrum that is 1.2-1.6 mm long, cylinder narrowly lacerate-fringed at base, segments ± regularly narrow-trapezoidal, 0.3 mm long, pendent, some slightly inflated above, ± broken off, calyptra shiny and golden-brown to smoky-brown, somewhat transluscent, with white lacerations in some, smooth; in transverse section cylinder composed of 2-3(4) layers of cells with very thick walls, fringe is of 1 row of cells, walls exceptionally thickened; in superficial view fringe cells short- to long-oblong. Chromosome number n=13 (Horton 1979a).

Habitat: The fundamental factor limiting the occurrence of E. longicolla is probably substrate-type. Throughout its range, populations grow only on very strongly calcareous substrates. This has been reported by Persson and Gjaerevoll (1957), Crum (1960-61) and Horton (1979a) for North America, and by Limpricht (1890) and Amann (1912) for Europe. The results of analyses of soil samples gathered with collections of E. longicolla in western North America bear out the above reports. Encalypta longicolla has been found on substrates with a range of pH from 6.9 to 7.9 (n=40 from 17 localities) and a mean of 7.3 (s.d.=±0.30) (Fig. 300). Limpricht (1890) was the first to report that E. longicolla occurs on humic soil, and this was later noted by Amann (1912), and Persson and Gjaerevoll (1957). In my experience in western North America, E. longicolla does not grow on mineral soil. There is always a high humic content.

In Europe and northwestern North America, E. longicolla generally is found only in montane habitats. However, it is also known from two localities in arctic regions of North America. Populations of E. longicolla are found on seepy soil of tundra slopes, characteristically on the sheltered edge of small solifluction lobes, and on ledges of rock outcrops. Many of the populations consist solely of E. longicolla and the plants form "kleinen Häufchen.", as Bruch (1832) originally described them. In some populations, other such mesic calciphiles as *Encalypta alpina*, *Blepharostoma trichophyllum* (L.) Dum., *Cyrtomnium hymenophylloides* (Hüb.) Kop., *C. hymenophyllum* (B.S.G.) Holmen, *Ditrichum flexicaule* (Schwaegr.) Hampe, *Encalypta alpina*, *Meesia uliginosa sendtneriana* (B.S.G.) Limpr., *Orthothecium strictum* Lor. and *Pleuroclada albescens* (Hook.) Spruce are associated with plants of *E. longicolla*.

Distribution: *Encalypta longicolla* is reported from northwestern and eastern North America, and from Svalbard, Scandinavia and the Alps in central Europe (Fig. 111). In North America, it is known from Alaska in the Brooks Range and the White Mountains near Fairbanks; from the Yukon Territory in the British, Ogilvie, southern Richardson and Selwyn Mountains; from the Northwest Territories on Banks Island and the mouth of the Coppermine River, and in the Mackenzie Mountains; from northcentral British Columbia in the Cassiar Mountains; from western Alberta from the Rocky Mountains at the Columbia Icefield; and from western Newfoundland from Tuckers Head, Bonne Bay (Fig. 112). In Europe, *E. longicolla* has just been reported from the Torneträsk area in northern Sweden (Horton 1982). It is also known from the Jura Mountains, and the Alps in Switzerland, Austria, southern West Germany, northern Italy and northwestern Jugoslavia (Fig. 113).

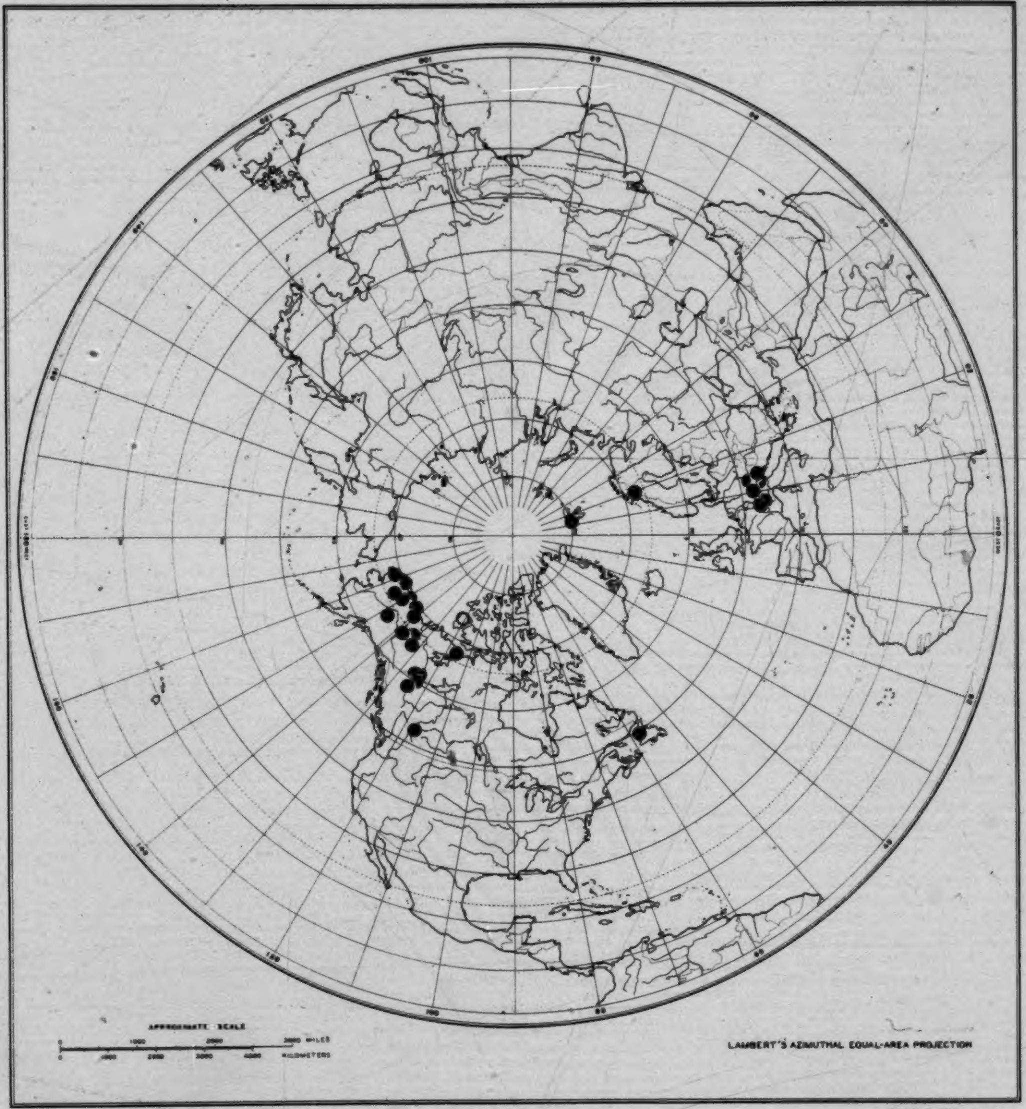
The specimen of *E. longicolla* from northern Sweden was only recently collected and confirms the occurrence of this rare species in Scandinavia. Earlier, Schimper (1876) reported *E. longicolla* from the mountains of Norway, but did not state the locality more specifically and did not cite a collector. There is presently no specimen in his herbarium to confirm this record. Lindberg (1879) excluded *E. longicolla* from the moss flora of Scandinavia and considered the Schimper specimen to be misdetermined.

Encalypta longicolla is very rare, particularly in Europe, but also in North America. However, it is quite frequent locally, and there are numerous collections from a single locality in many instances. For example, there are many collections from Chasseron in the Jura Mountains. Similarly, there was enough *E. longicolla* at the site in western Alberta to collect an exsiccata of 50 specimens (Horton 1979a) and there are a number of collections in different herbaria from the Summit Lake area in northcentral British Columbia.

Figure 111. Distribution of *Encalypta longicolla*.

WORLD, NORTHERN HEMISPHERE

No. 201PN



GOODE'S SERIES OF BASE MAPS
HENRY M. LEPPARD, EDITOR

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Figure 112. Distribution of *Encalypta longicolla* in North America.

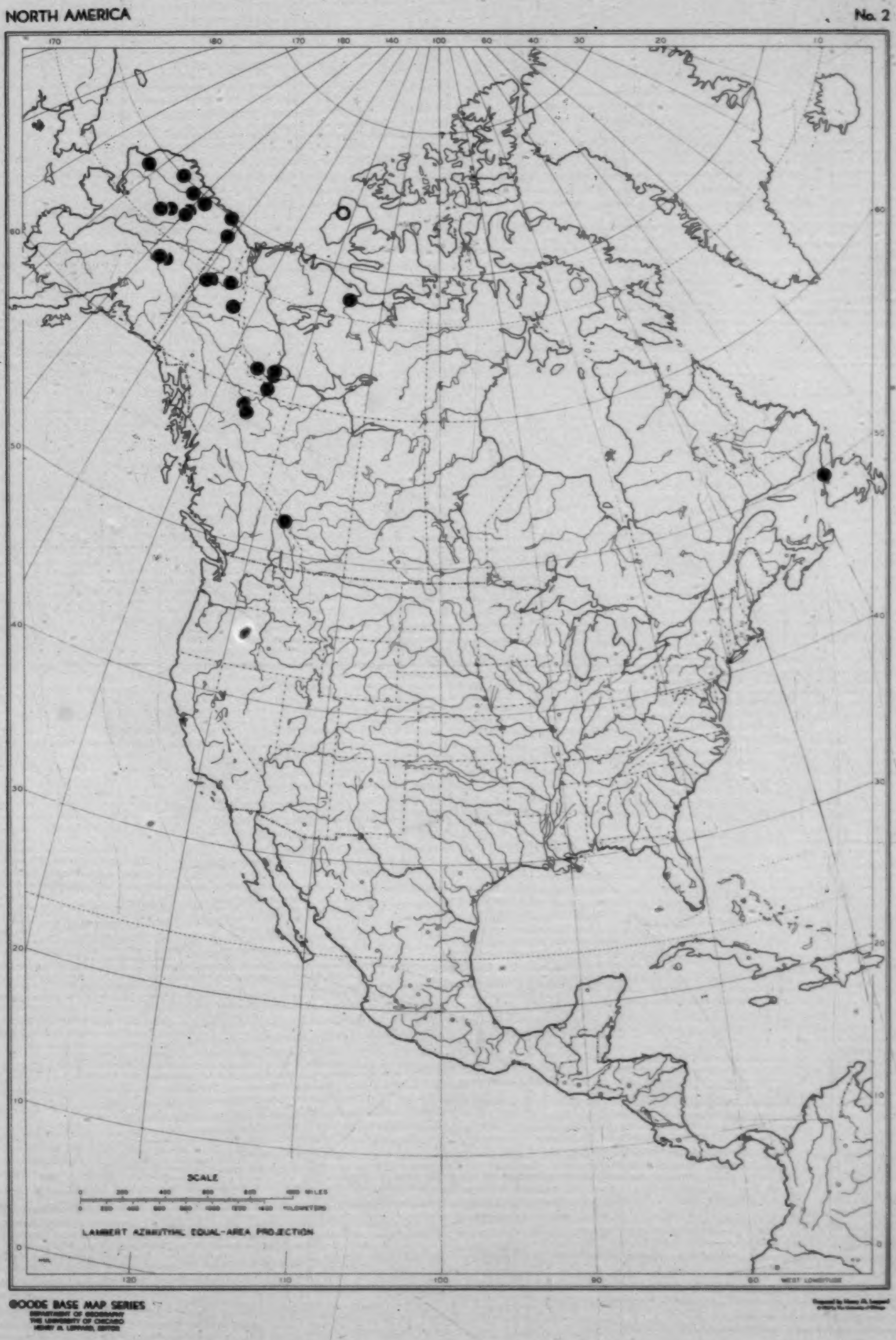
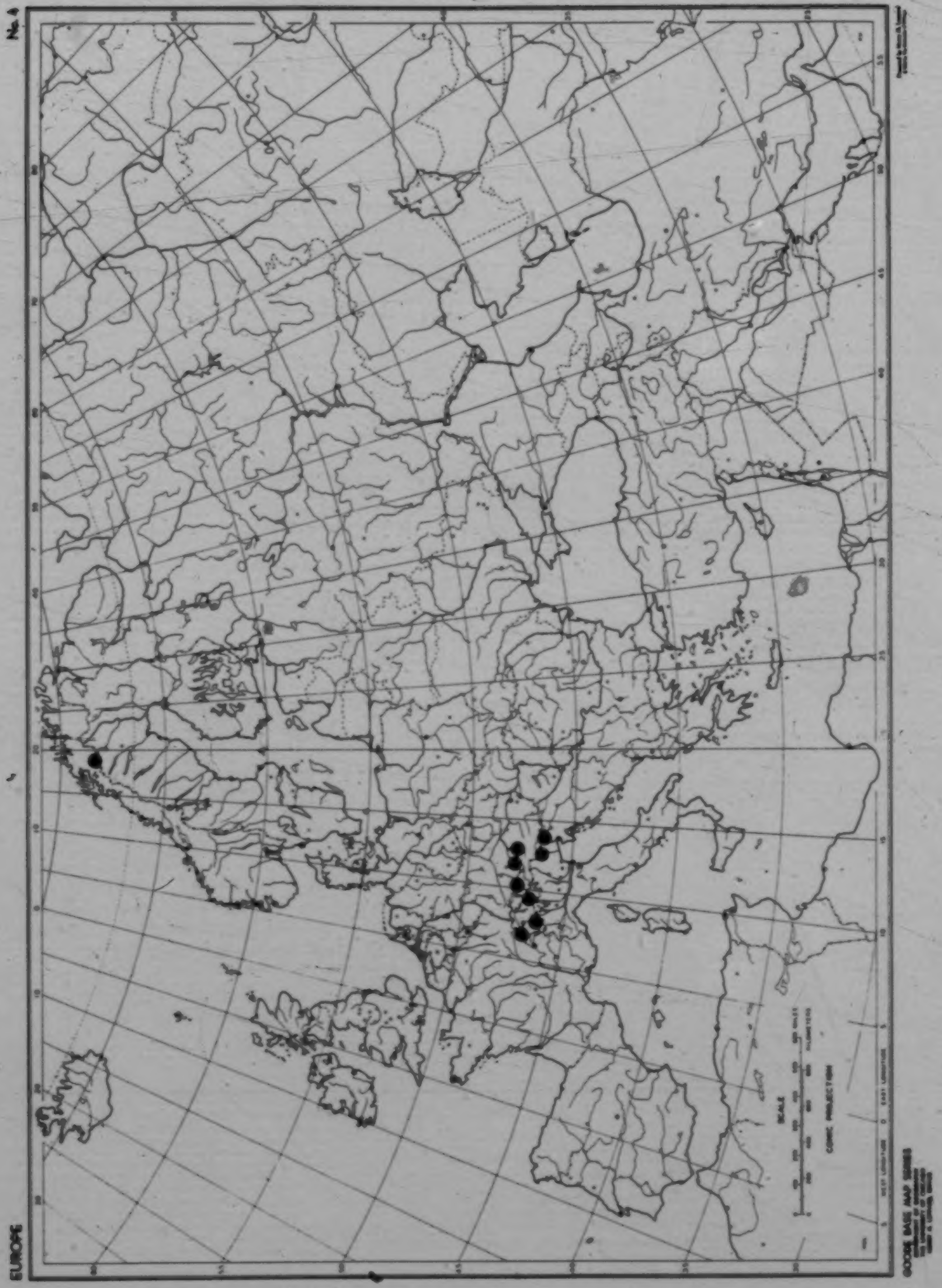

NORTH AMERICA
No. 2
SCALE
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

Figure 113. Distribution of _Encalypta_ _longicolla_ in Europe.


No. 4
EUROPE
SCALE
CONIC PROJECTION
WEST LONGITUDE
EAST LONGITUDE
GOODE BASE MAP SERIES

In 1926, Herzog reported *E. longicolla* to be endemic to the Alps and the Jura Mountains. However, in 1957, Persson and Gjaerevoll reported a specimen collected in the White Mountains of Alaska and noted that Steere had earlier collected it in the Brooks Range in 1951. Crum (1960-61) reported a fourth North American locality in the Summit Lake area of northcentral British Columbia and he suggested that the pattern of disjunction of *E. longicolla* indicated that this species had survived the Pleistocene glaciations *in situ*. Further North American records are reported in Horton (1979a), including one disjunct locality at the Columbia Icefields in western Alberta. Horton (1979a) concurred with Crum's interpretation of *E. longicolla* as a refugial species and suggested that the populations at the Columbia Icefields might be the result of post-glacial long-distance dispersal from Beringian refugia in the north. It is also possible that populations of *E. longicolla* survived in local refugia in the southern Canadian Rocky Mountains (see Packer & Vitt 1974, Horton 1981a). The occurrence of *E. longicolla* in the Coppermine area of the Northwest Territories, which was extensively glaciated (Prest 1969), is further evidence of post-glacial dispersal (Horton 1982). In western Newfoundland, *E. longicolla* is reported to be from an area that was ice-free through much of Wisconsinan times (Belland & Brassard 1980). The concentration of localities in northern Alaska-Yukon-Northwest Territories and in the Alps suggest that most of the popuations of *E. longicolla* survived in unglaciated areas during the Wisconsin and the few outlying populations in northern Sweden, Svalbard, western Newfoundland and western Alberta perhaps are derived from populations that survived in isolated refugia.

Phylogenetic Relationships: *Encalypta longicolla* is so distinctly differentiated from other species of *Encalypta* in the features that generally indicate relationships that it is difficult to make a suggestion as to the affinities of this species. The well-defined, long neck of the capsule and the exceptionally large, irregular spores are unique to this species. The fused, double peristome is characteristic also of *E. affinis* and *E. brevicolla*, but the dome-shaped habit of the teeth in *E. longicolla* is quite different than the more-or-less erect habit of the former species. Relatively broad, smooth capsules with a turgid appearance are characteristic of *E. brevicolla* as they are of *E. longicolla*. The dark-orange, strongly thickened transverse walls of the basal laminal cells in *E. longicolla* are reminiscent of those of E. affinis. However, in calyptra characteristics E. longicolla is quite different from E. affinis and E. brevicolla, and E. longicolla occurs only on calcareous substrates, while the latter species are either restricted to acidic substrates (E. brevicolla) or are tolerant of subneutral conditions (E. affinis).

As noted under Diagnosis and Differentiation, the calyptra of E. longicolla is virtually indistinguishable from that of E. alpina and both species are restricted to mesic, calcareous substrates. However, in most other structural characteristics these two species are very different so it is difficult to assess the significance of the parallelism in calyptrae and habitat.

Specimens Examined: ALA (9), ALTA (145), BM (19), BP (3), CANM (2), FI (5), G (2), H (9), H-Sol (2), Priv. Herb. D. G. Horton (76), JE (20), LAU (30), MICH (1), NY (18), O (4), PC (3), RO (1), S (17), TRH (6), UBC (9), Z (8).

ENCALYPTA ALPINA Smith in Smith et Sowerby,

Engl. Bot. 20: 1419 + 1 pl. 1805.

Figs. 79, 114-121.

Type: "Gathered on rocks about the very summit of Ben Lawers by Mr. G. Don in October 1804." (Lectotype: "Encalypta alpina habetat [sic] rocks on the summit of Ben Lawers Oct. 180[?] Mt. Don" BM-Turner!).

Encalypta ciliata Hedw. var. alpina (Sm.) Hook. et Tayl., Musc. Brit. 35. 1818.

Encalypta fimbriata Lam. et DC. var. alpina (Sm.) Hook. et Tayl. ex Brid., Bryol. Univ. 1: 143. 1826. Nom. inval.

Encalypta commutata Nees, Hornsch. et Sturm, Bryol. Germ. 2(1): 46, pl. 15, Fig. 4. 1827. Types: "Wächst auf dem Glockner in der Nähe der Gletscher (Schwaegrichen), an feuchten, felsigten, vom Grase entblösten Stellen auf Pasterze, der Leiter, dem Tauern und andern Alpen um Heiligenblut und dem Rathhausberg und Bockhardt in der Gastein (Hoppe! Funck! Laurer! Hsch.), und an Felsen der Messerlingwand auf dem Windischmattreyer Tauern (Hsch.), um München in schattigen Waldungen auf

Kalkfelsen (*Kittel*?)." (Lectotype: "Encalypta commutata Hrnsch In alpe Pasterze et in mun's antiquis alpinis" GZU–Hoppe!).

Encalypta lacera De Not., Mem. Reale Accad. Sci. Torino 39: 245. 1836. Type: "In alpibus supra *Reme*, regione nivali superata legit Dom. COMBA." (Holotype: "Encalypta lacera DNtrs. In alpibus supra Reme legit Comba DNtrs." RO!).

Encalypta caucasica Ruprecht *ex* Weinmann, Bull. Soc. Imp. Naturalists Moscou 19: 521. 1846. Type: "In monte Kasbeck altit. 1526' prope nives liquescentes Augusto." (Lectotype: "*Leersia* alpina (*Sm.*) =Enc. caucasica *Rupr.*! Fl. caucas. in m. Kasbek, altit. 1526 hexap., prope nivas liquesc. 13/8 44 *Rolenati*" H–Sol!).

Leersia alpina (Sm.) Lindb., Musci Scand. 20. 1879. *Nom. inval.*

Leersia alpina (Sm.) Lindb. var. *imberbis* Lindb. *ex* Braithw., Brit. Moss Fl. 1: 280. 42. 1887. Type: "Ben Laoigh, Perthshire (*Holt*, July, 1880)" (Lectotype: "Leersia vulgaris var. β quid? an species propria Br. Moss Fl. Tab. 42, B.J. Ben Laiogh – Perth$^{\text{sh.}}$ Holt. July/80 *L. alpina* var. *imberbis Lindb.*" S–Möll.!). *Nom. inval.*

Encalypta commutata Nees, Hornsch. *et* Sturm var. *fimbriata* Kindb., Forh. Vidensk. –Selsk. Christiana 1888(6): 21. 1888. Type "Knudsho" (No type found in S).

Encalypta commutata Nees, Hornsch. *et* Sturm var. *imberbis* (Lindb. *ex* Braithw.) Dix., Stud. Handb. Brit. Moss. ed. 1: 228. 1896.

Encalypta giraldii C. Müll., Nuovo Giorn. Bot. Ital. n. s. 5(2): 173. 1898. Type: "China interior, prov. Schen-si sept., in monte Tui-kio-san, Oct. 1896: *J. Giraldi*...." (Lectotype: "China interior, provincia Schen-si sept. in monte Tui-Kio-san 20 Oct. 1896 Giraldi" H–Br!; Isotype: BM!).

Encalypta commutata Nees, Hornsch. *et* Sturm var. *striata* Meyl., Rev. Bryol. Lichenol. 39: 18. 1912. Type: "au sommet du Chasseron, vers 1.600 m." (Holotype: "Encalypta commutata var: striata var. nov. Chasseron. 1600 m. Sept. 1910. leg Ch Meylan" LAU!).

Encalypta commutata Nees, Hornsch. *et* Sturm var. *serrata* Meyl. *ex* Syd., Bot. Jahresber. (Just) 40(1): 72. 1913. *Nom. inval. err. pro E. commutata* var. *striata* Meyl.

Encalypta rhaptocarpa Schwaegr. var. *serrata* Meyl. *ex* Syd., Bot. Jahresber. (Just) 40(1): 58. 1916. *Nom. inval. err. pro E. commutata* var. *striata* Meyl.

Encalypta commutata Nees, Hornsch. *et* Sturm var. *rhaptotheca* Amann *et* Meyl., Fl. Mouss. Suisse 1: 104. 1919. Type: none cited.

Encalypta alpina Sm. var. *imberbis* (Lindb. *ex* Braithw.) P. Rich. *et* Wallace, Trans. Brit. Bryol. Soc. 1(4): ix. 195.

Encalypta alpina Sm. var. *fimbriata* (Kindb.) Podp., Consp. 160. 1954.

Nomenclatural Notes: (1) Capsules of *E. alpina* consistently lack a peristome, yet Smith (1805) in his description of this species referred to a peristome "...of 16 linear upright teeth.". There is presently no specimen of *E. alpina* in the Smith herbarium at the Linnean Society of London (T. O'Grady, Executive Secretary *in litt.*). Furthermore, Mr. O'Grady has informed me that when a specimen is present in the Smith herbarium, the citation in English Botany (where the original description of *E. alpina* was published) included the notation 'our specimen' or 'Specimens have been sent by...'. Such a notation is not included with the citation of the type specimen of *E. alpina*, so it is possible that this specimen never was in Smith's herbarium. Smith reported G. Don as the collector of the specimen of *E. alpina* and E, OXF and BM are cited by Sayre (1977) as repositories for the Don herbarium. There is no Don specimen of *E. alpina* in E; however, in the Turner-Hooker herbarium in BM, there is such a specimen, which has been selected as the lectotype. This specimen presently consists solely of *E. alpina*, so it is difficult to understand the reference to a peristome in the original description, unless the specimen formerly consisted of a mixture. When Nees, Hornschuch and Sturm (1827) described *E. commutata*, they referred to Sowerby's plate of *E. alpina*, which accompanied the original description, but did not illustrate a peristome, and omitted reference to Smith's description. In contrast, in their descriptions of other species of *Encalypta*, Nees, Hornschuch and Sturm did cite Smith, so in the instance with *E. alpina* it may have been a purposeful omission. One can speculate that they found the description to be incorrect in this feature and therefore omitted reference to it.

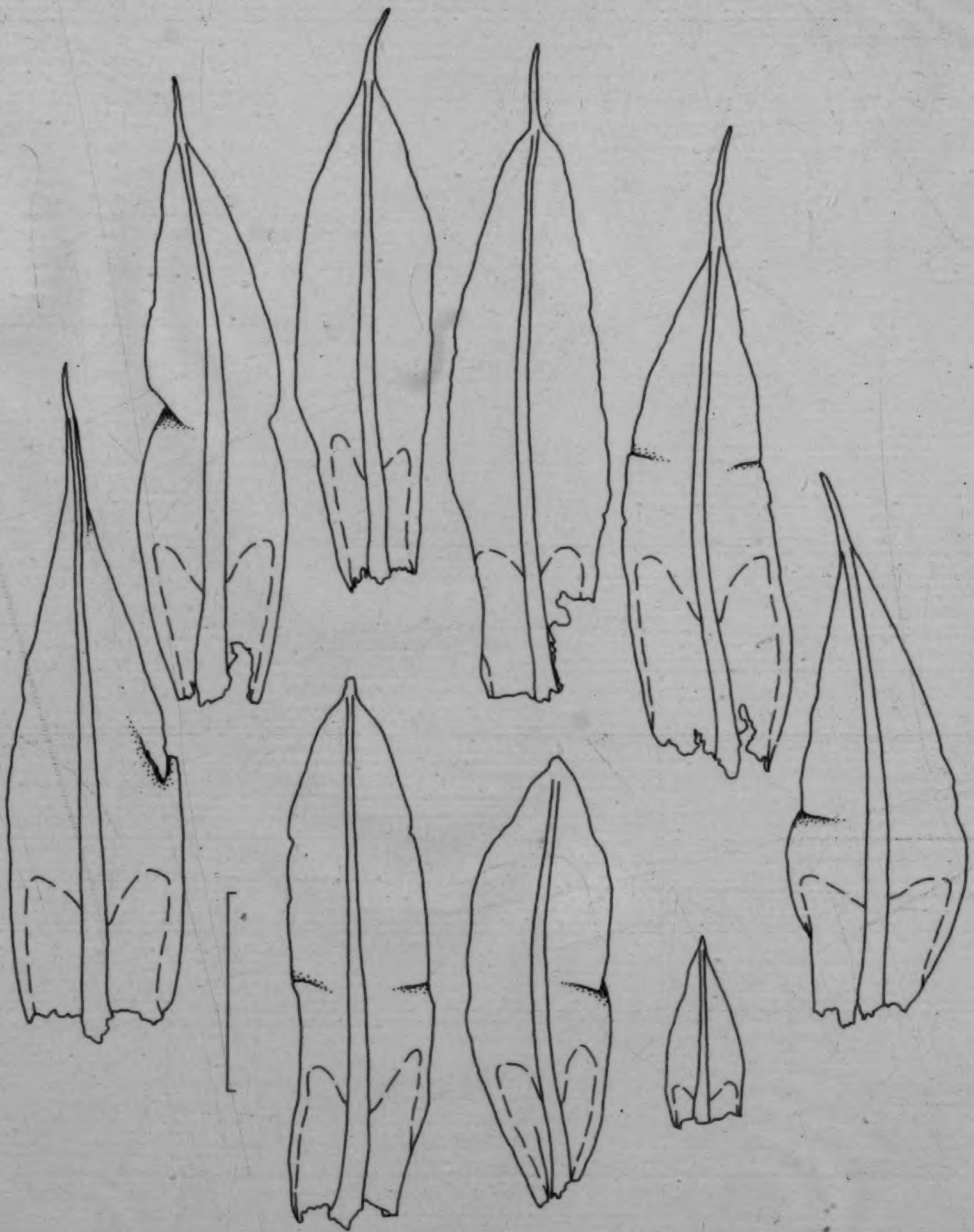
It is clear from Sir Joseph Dalton Hooker's diary (Huxley 1918) that James Edward Smith was a close acquaintance of both his father, William Jackson Hooker, and his maternal grandfather, Dawson Turner. Therefore, it is possible that this specimen in BM is actually the original specimen that Smith described, or it may be a duplicate given to Turner by Don. In any event, the taxonomic concept of *E. alpina* is well established historically and as the type specimen fits this concept, I see no reason to consider this specimen as unsuitable for a lectotype, despite the incongruency with the original description.

(2) See Variation for a discussion of Leersia alpina var. imberbis.

Diagnosis and Differentiation: Encalypta alpina is differentiated from all other species of Encalypta by the narrowly acute and stoutly apiculate apex of the leaves. Another particularly striking characteristic is that the golden to golden-brown, opaque calyptra is glossy. As well, the calyptra is distinctly, but only slightly, narrowed to a relatively short rostrum. The base of the calyptra cylinder is lacerate with long, more-or-less incurved segments that are pale-brown initially, but with age become white and then are generally broken off leaving an erose, white border. The gymnostomous capsules are narrowly cylindric and sharply contracted at or just below the mouth, and in many populations there is a white rim of tissue just inside the mouth. The shiny seta is dark-red to almost black and the stoutly apiculate leaves have a similarly shiny, but dark-brown costa (except in the uppermost leaves where the costa is green). Plants of E. alpina have a very neat, almost rather sparse appearance attributable to the clasping leaves that are hardly twisted in most populations. There is an overall impression of shininess derived from the calyptra, seta and the costa. Microscopically, E. alpina is characterized by upper leaf cells that tend to be slightly smaller than in most other species of Encalypta. However, the size of the cells is difficult to determine because the vertical walls of the upper leaf cells are obscurved by the dense, "c"-shaped papillae on the outer walls and it is actually this obscurity of the upper leaf cells that is a better differentiating feature than the size. The basal leaf cells are prominent with both the transverse and longitudinal walls colored dark-orange. Also, there is a clearly defined basal marginal border of elongate, yellowish cells. The abaxial surface of the costa is smooth and there are two to three rows of stereids in a transverse section. The spores are irregularly, finely gemmate and with SEM the surface of the gemmae appears very irregular.

Encalypta alpina might be confused with E. mutica, E. longicolla, E. procera or E. rhaptocarpa. Encalypta mutica resembles E. alpina in the lack of a peristome, and the shape and coloration of the capsules is virtually indistinguishable from some that occur in E. alpina. Also, the spores of E. mutica are very similar to those of E. alpina in the

Figure 114. Variation in Leaves of *Encalypta* *alpina*. Scale=1 mm. Note 'atypical' muticous leaves from type of the variety *imberbis* (left), a Yukon population (centre) and an Arctic population (right).



Figures 115-120. Encalypta alpina.

Figs. 115-118. Spores.

Figs. 115-116. Distal surface.

Fig. 115. Scale=10 μm.

Fig. 116. Scale=4 μm.

Figs. 117-118. Proximal surface.

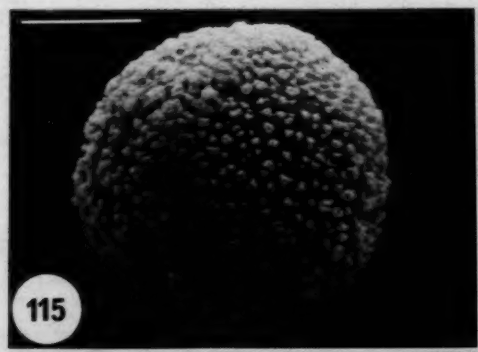
Fig. 117. Scale=10 μm.

Fig. 118. Scale=4 μm.

Figs. 119-120. Capsule mouth with 'hymenium'.

Fig. 119. Scale=100 μm.

Fig. 120. Scale=40 μm.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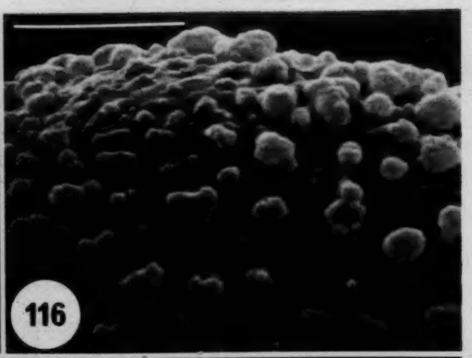
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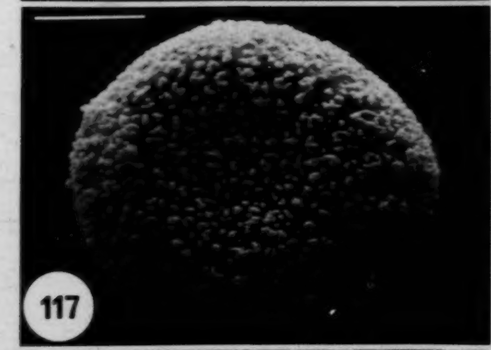
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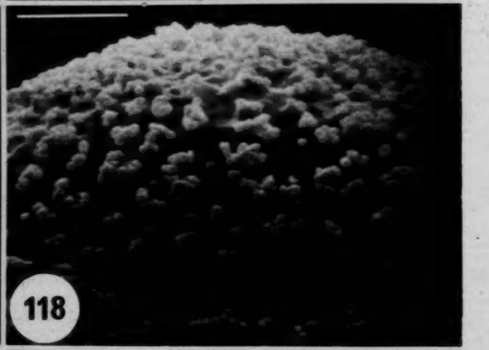
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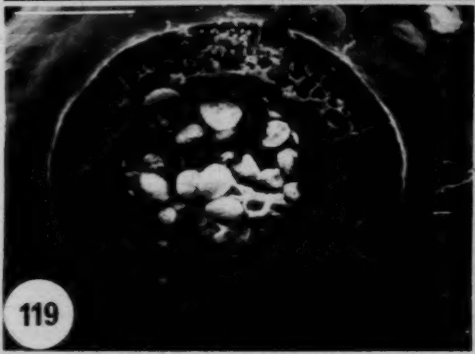
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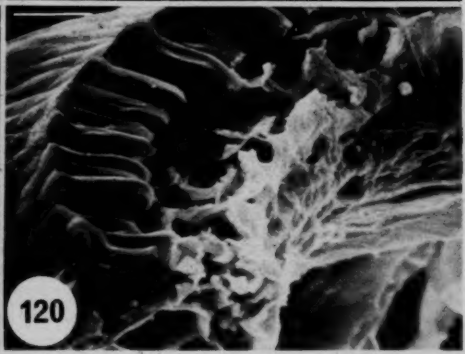
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sculpture of the exine. *Encalypta mutica* is best distinguished by the consistently muticous leaves with inconspicuous basal cells. In both *E. longicolla* and *E. procera*, the calyptrae are similar in shape and coloration to those of *E. alpina*. *Encalypta longicolla* can be differentiated by the long, dark-red peristome teeth and leaves with long, hyaline hair-points. The calyptra of *E. procera* is papillose, at least in the upper part, and there is a long, double peristome present on the spirally twisted capsules. *Encalypta procera* can also be distinguished by leaves with recurved margins and the brood bodies that commonly occur on sterile plants.

Description: *Plants* to 50 mm tall, light-green to olive-green with yellow tones above, brown below, ± branched. *Stem* in transverse section with central strand undifferentiated in most populations, when present, cells small, walls thin and hyaline. *Brood bodies* absent. *Axillary hairs* sparse. *Leaves* when dry incurved and only very slightly twisted in most populations, somewhat twisted in very few, laminae conduplicate to inflexed; (1.0)2.3–3.4(4.0) mm long, (0.4)0.7–1.0 mm wide, ovate-lanceolate, narrowly ovate-lanceolate or narrowly ovate-oblong, apex very gradually narrowed and narrowly acute, stoutly apiculate to stoutly short hair-pointed (≤ 1 mm long) in virtually all populations, apiculus or hair-point yellow, very few populations with apex muticous; *margins* plane. *Costa* excurrent, subpercurrent in very few populations, abaxial surface keeled, shiny, green to dark-brown to dark-red, smooth; in transverse section with 2–3 rows ventral cells, begleiters undifferentiated or some with 2 or 3, 2–3 rows of stereids. *Upper laminal cells* 7–12(14) μm wide, 7–12(16) μm long, with 2–5 papillae, each ± "c"-shaped; *upper marginal cells* (9)12–14 μm wide, 7–12 μm long; *transitional cells* with walls smooth above basal cells on abaxial surface, on adaxial surface walls smooth well above basal cells; *basal laminal cells* 40–90 μm long, 9–23 μm wide, prominent, transverse walls dark-orange, longitudinal walls dark-orange, superficial walls smooth, irregularly ± perforated; *basal marginal cells* yellowish, distinctly differentiated in rows. Goniautoicous. *Perichaetial leaves* sheath-like and broadly ovate-lanceolate; *perigonial leaves* to 1.3 mm long, sheath-like and broadly ovate-lanceolate below; *perigonial paraphyses* with upper cells divided, walls smooth.

Seta 6-12 mm long, flexuose in most populations, to erect, ± strongly and tightly twisted dextrorsely above middle, shiny and dark-red to blackish; in transverse section 185-210 μm in diameter. Capsule (1.2)1.5-3.0 mm long, when dry cylindric to narrowly-cylindric with 5-6 very slight ± indistinct longitudinal ridges, ± strongly contracted at mouth or just below mouth, slightly puckered at base and abruptly contracted to seta, delicately puckered throughout, golden-brown with dark-red mouth and many with very faint dark-red coloration of ridges, when young golden-green with dark-red or orange rim, when old ± longitudinally plicate and collapsed; exothecial cells 60-126 μm long, 12-28 μm wide, in ± regular, longitudinal rows, in transverse section walls slightly and evenly thickened on external surface, 1 m thick, with strong corner thickenings at junction of outer periclinal and radial-longitudinal walls, 7 μm thick; rim cells in 1-2 irregular rows, 12-18 μm wide, 7-23 μm long, walls somewhat evenly thickened; stomata superficial, restricted to capsule base, 32-58 μm long, 30-46 μm wide. Peristome absent; narrow rim of white tissue at mouth may represent hymenium. Operculum 1.5 mm long, plane-convex and rostrate. Annulus undifferentiated. Spores pale-brown, paraisopolar, in polar view radially symmetric and circular, 28-37 μm, in equatorial view polarly asymmetric and concave-convex, 29-37 μm X 23 μm, ± densely, irregularly gemmate, gemmae very small to moderate size (ca. 1.0-2.3 μm), low rounded to elongate and somewhat irregular, with SEM gemmae covered with granular deposition. Calyptra (3.3)4.0-7.0 mm long, cylindric to narrowly-cylindric, distinctly but only slightly contracted to slightly curved or erect rostrum that is (0.9)1.2-1.7 mm long, cylinder smooth to faintly puckered, lacerate basally, segments 0.4 mm long, ± irregularly trapezoidal, broken off with age, pendent to ± incurved, calyptra golden to golden-brown, dark-brown distally, with brownish to white lacerations, glossy, opaque, smooth; in transverse section cylinder with 3 rows of cells with very thick walls, lacerations with 1 rows of cells, walls very strongly thickened; in superficial view cells of lacerate portion quadrate to oblong. Chromosome number n=14 (Steere 1954).

Habitat: Populations of *E. alpina* are restricted to seepy or very mesic habitats. They commonly occur intermixed in lush mats of bryophytes that drape down over the top of rock outcrops exposed on steep slopes from the montane zone up into alpine tundra. In such places, the plants of *E. alpina* generally are situated close to the tip of the mat where the water seepage accumulates. It also characteristically occurs on seepy patches of exposed soil, particularly in the spray zone or in small rivulets associated with waterfalls. In contrast to *Bryobrittonia* and such other species of *Encalypta* as *E. procera* that also characteristically grow in mesic habitats, *E. alpina* is not found on soil along river banks, in my experience, although it does occur on soil around the margins of lakes. Limpricht (1890) described *E. alpina* (as *E. commutata*) as an "Echtes Hochalpenmoos!". This characterization is particularly apt when taken in the broader sense of having an affinity for tundra habitats. *Encalypta alpina* is one of the few species of *Encalypta* that occurs as far north as the high arctic in the Canadian Arctic Archipelago. In arctic regions populations occur in mesic sedge meadows, intermixed in characteristically diverse assemblages of bryophytes. Rather consistent associates of *E. alpina* include *Blepharostoma trichophyllum* (L.) Dum., *Distichium capillaceum* (Hedw.) B.S.G., *Ditrichum flexicaule* (Schwaegr.) Hampe, *Encalypta procera*, *Meesia uliginosa* Hedw., *Myurella julacea* (Schwaegr.) B.S.G., *M. tenerrima* (Brid.) Lindb., *Orthothecium intricatum* (C. J. Hartm.) B.S.G. and *O. strictum* Lor. Other more sporadic associates also reflect the mesic nature of the habitat and these include *Arnellia fennica* (Gott.) Lindb., *Campylium stellatum* (Hedw.) C. Jens., *Cyrtomnium hymenophyllum* (B.S.G.) Holmen, *Distichium inclinatum* (Hedw.) B.S.G., *Drepanocladus uncinatus* (Hedw.) Warnst., *Encalypta rhaptocarpa*, Eurhynchium pulchellum (Hedw.) Jenn., *Hylocomnium pyrenaicum* (Spruce) Lindb., *Hypnum bambergeri* Schimp., *H. revolutum* (Mitt.) Lindb., *Marsupella revoluta* (Nees) Dum., *Mnium thomsonii* Schimp., *Plagiochila asplenioides* (L.) Dum., *Thuidium abietinum* (Hedw.) B.S.G., *Timmia austriaca* Hedw., *Tortella tortuosa* (Hedw.) Limpr. and *Tritomaria exsectiformis* (Breidl.) Loeske.

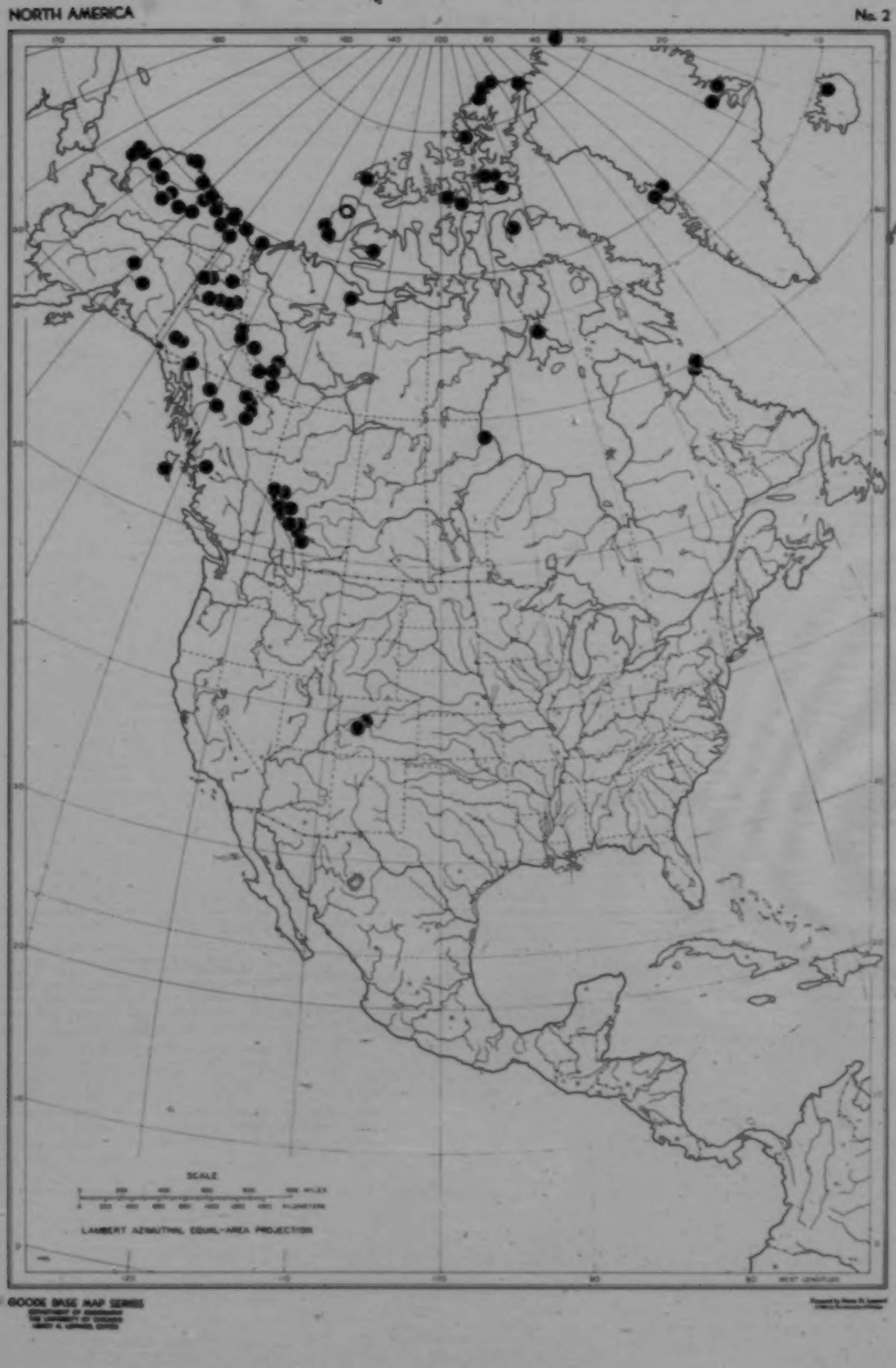
As is apparent from the foregoing lists of associates, populations of *E. alpina* generally occur where the substrate is relatively calcareous. Limpricht (1890) and Martensson (1956) reported *E. alpina* to be associated with calcareous substrates in central and northern Europe, respectively. However, in western North America, populations have been found growing on soil with a range of pH from 6.2–7.4 (n=36 from 20 different localities) and a mean of 7.0 (s.d.=±0.59) (Fig. 300). Similarly, the range in Ca^{++} and Mg^{++} concentrations is considerable, but the means are higher than for most species of Encalyptaceae (Figs. 301–302, Table 9). It should be noted that the lower end of the pH range indicates tolerance of slightly acidic conditions. *Encalypta alpina* is not uncommon where the rocks are granite. Therefore, it is to be sought after in seepy habitats, particularly where the substrate is calcareous. However, substrate-type is considered to be a less important factor in determining the occurrence of *E. alpina* than is moisture.

Distribution: *Encalypta alpina* has a circumpolar, montane-arctic distribution. In North America, most collections are from the Western Cordillera with some others known from widespread localities in the Canadian Arctic, Greenland and Iceland. Along the Cordillera, *E. alpina* is reported from Alaska in the Brooks and Alaska Ranges; from the Yukon Territory from Herschel Island, and the British, Ogilvie, southern Richardson, Wernecke and St. Elias Mountains; from the western Northwest Territories in the Mackenzie Delta and the Mackenzie Mountains; from British Columbia in the Cassiar and Rocky Mountains, Moresby Island and the Bulkley Ranges; from Alberta in the Rocky Mountains; and from what presently appears to be a disjunct locality in the Rocky Mountains in Colorado. In arctic and subarctic regions, *E. alpina* has been collected in the Northwest Territories at Coppermine, Bathurst Inlet, on Prince Patrick, Banks, Victoria, Seymour, Bathurst, Cornwallis, Ellesmere, and Devon Islands. Kuc (1973a) reported it from Axel Heiberg Island (indicated on Fig. by an open circle because the specimens have not been available to me for verification). *Encalypta alpina* is also known from the Borden Peninsula of Baffin Island, and Southhampton Island; in Manitoba in the Churchill area; and in Newfoundland in northern Labrador. It is also reported from Greenland on the east, west and north coasts, and from northeastern Iceland (Fig. 121).

Encalypta alpina is not uncommon within its range, but the populations are generally not particularly abundant. It is restricted to montane and arctic habitats, and is one of the few species of *Encalypta* that occurs in the High Arctic. Although the number of localities presently known for *E. alpina* in the Canadian Arctic are relatively few, this species is probably more-or-less ubiquitous throughout the Arctic Archipelago.

Variation: *Encalypta alpina* is a well-defined species that shows little interpopulational variation in the features noted under Diagnosis and Differentiation. In particular, the leaves

Figure 121. Distribution of *Encalypta alpina* in North America.


NORTH AMERICA
No. 2
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES

are consistently (with the exception of some arctic populations, see below) narrowly acute with the costa excurrent in a stout, yellow apiculus. However, one population from the eastern Yukon Territory (Horton 14662, ALTA) has muticous leaves with a subpercurrent costa (Fig. 114 – lower centre). Similarly, Leersia alpina var. imberbis was described by Braithwaite on the basis of a specimen from Britain with leaves lacking an apiculus. In this specimen, there is some variation and some of the leaves are muticous with an acute apex while others are muticous with a broadly mucronate apex (Fig. 114 – lower left). I have been unable to find any other discernible differences in the character-states of the plants in these anomalous populations. Therefore, I feel that these should presently be regarded as possibly representing either a genetic or developmental aberration or an environmental modification, and should not be given any formal nomenclatural recognition.

Some arctic populations of E. alpina consist of very small, stunted plants. The leaves of such plants generally lack an apiculus (Fig. 114 – lower right). In some of these it appears to have been abraded away; in others it appears not to have developed. Other arctic populations consist of plants with a well-developed apiculus. Therefore, I have concluded that the lack of an apiculus in these arctic populations is an environmental modification and not worthy of formal taxonomic recognition.

Phylogenetic Relationships: As with E. mutica, there is no particular species of Encalypta that E. alpina appears to be closely related to. However, several features indicate distant connections with E. procera or a species with similar characteristics. Dark coloration of the long calyptra, the rostrum that is only slightly defined and the lacerate cylinder typify E. procera as well. Also, the narrow capsule and dark seta that is relatively long in some populations parallel the conditions in E. procera. Coloration of vegetative plants is also similar. In E. alpina the leaves are rich green with dark-red tones imparted by the basal laminal cells and the abaxial surface of the costa. The spores of E. alpina are indistinctly heteropolar with small gemmae, while those of E. procera are isopolar and finely scabrate.

Specimens Examined: ALA (28), ALTA (270), BM (2), CANM (25), COLO (2), H (2), H-Br

(18), H–Sol (30), NFLD (13), NY (80), S (1), UBC (25).

ENCALYPTA MUTICA Hagen,

Tromso Mus. Aarsh. 21–22(1): 91, pl. 1, fig. 4. 1899.

Figs. 122–133.

Types: "Sondre Trondhjems amt, Opdal, Varstigen 1886: Kaur.", "Strinden, Ladehammeren auf Chloritschiefer in Nordlage nur wenige m. über dem Fjorde 16/8 1895 mit theilweise entdeckelten Früchten: H.", "No. Saltdalen, Nedre Bergulnesli 100 m. 2/8 1889: F.", "Vik; Skjerstad, an der Nordseite von Nedrevatnet bei ca. 100 m. Meereshöhe auf erdbedeckten Felsen, an den beiden letzten Stellen mit E. rhabdocarpa vermengt: H." (Lectotype: "Encalypta mutica Hag. n. sp. Sondre Trondhjems amt, Strinden Ladehammeren altit. mtr. ca. 10–20 16/8 1895 leg. I. H." TRH!; Isotypes: JE!, O!; Syntypes: O (2 specimens (in part))!, TRH (in part)!).

Encalypta ciliata Hedw. var. minor Somm., Suppl. Fl. Lapp. 46. 1826. Type: "in collibus arenosis Saltdalen Nordlandiae." (Holotype: "Encalypta n. sp? ciliata β minor Somf. Saltd. i aren. rup. col. 10/18" O–Sommerfelt (in part)!).

Leersia mutica (Hag.) Möll., Bot. Not. 1907: 142. 1907. Nom. inval.

Nomenclatural Notes: Among the species of Encalypta presently recognized in the Northern Hemisphere north of 40°N, most were described before the middle of the 19th century. While E. mutica was not described as a species until 1899 (Hagen 1899), Sommerfelt had recognized it as early as 1826 when he described it as E. ciliata var. minor. The analogy to E. ciliata is an apt one, as the shape and coloration of the calyptra of E. mutica give it the appearance of a small form of E. ciliata. Hagen (1899) noted this similarity and reported that E. mutica can be easily mistaken for E. ciliata, particularly if no mature capsules are present. Actually, the resemblance ends with the calyptra, as Tuomikoski (1935) pointed out, and the characteristics of the leaves, which are in every detail quite different, should be enough to differentiate these two species.

Diagnosis and Differentiation: Tuomikoski (1939) aptly described E. mutica as "Die kleinste Encalypta-Art des Gebietes!" with reference to the Kuusamo area of Finland. Indeed, it is one of the tiniest species in the genus. Leaves are only one or two millimetres long, setae are eight (rarely 10) millimetres long or less and some are only two millimetres, capsules are one to two and one-half millimetres long, and calyptrae are four millimetres or less. It is not uncommon to find plants with calyptrae perfect in every detail, yet only two millimetres long, including the fringe. The shiny calyptra is cylindric to elliptic-cylindric and abruptly narrowed to the rostrum. At the base of the smooth and turgid-looking to faintly puckered cylinder, there is a slight constriction just above a narrow, but generally distinct horizontal or oblique expansion with a pendent, brownish to white fringe. The fringe segments are narrow and very precisely defined. Delicate striations give the pale-golden or golden-brown capsules a rather fragile appearance. A very narrow, crimson-red rim borders the gymnostomous mouth. The setae are shiny and dark-red to orange. The muticous and obtuse leaves are rather loosely erect and slightly twisted irregularly giving the plants an almost flaccid appearance. The laminal-type cells that cover the back of the costa in the upper part and the fact that the costa ends well below the apex of the leaf makes the costa somewhat inconspicuous. In contrast to many species of Encalypta, the costa does not protrude prominently on the abaxial surface of the leaves. Microscopically, E. mutica is defined by the costa that is papillose above the basal cells on the abaxial surface and consists of three or four rows of stereids in transverse section. The walls of the transitional cells are smooth well above the basal cells so that the basal cells appear very isolated from the papillose upper cells. The inconspicuous basal cells are characterized by transverse walls that are pale-orange and longitudinal walls that are hyaline. Spores of E. mutica are indistinctly polar and gemmate. With SEM the gemmae, which appear more-or-less smooth under the light microscope, prove to be minutely elaborated by an irregular microsculpture giving them an appearance reminiscent of the florets of a cauliflower (Horton & Murray 1976).

Among the gymnostomous species of Encalypta that might be confused with E. mutica, plants of E. brevipes are similarly quite small, but can be readily differentiated by the leaves with long, hyaline hair-points and smooth, turgid-looking capsules with a broad, crimson rim at the mouth. Some older capsules of E. alpina are virtually

Figures 122-126. **Encalypta mutica**. Scale=1 mm.

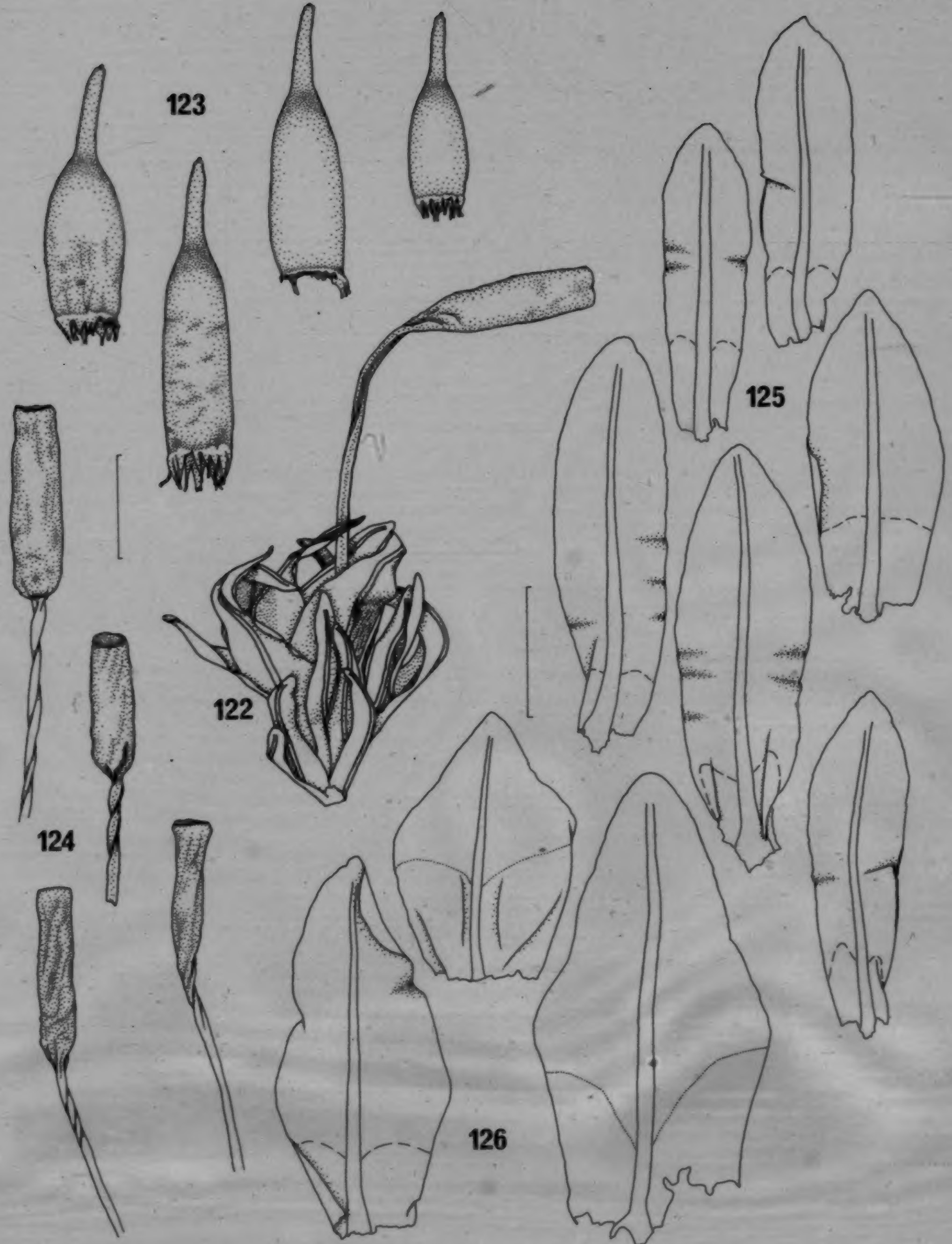
Fig. 122. Habit.

Fig. 123. Calyptrae.

Fig. 124. Capsules.

Fig. 125. Vegetative leaves.

Fig. 126. Perichaetial leaves.



Figures 127-130. Spores of Encalypta mutica.

Figs. 127–128. Distal surface.

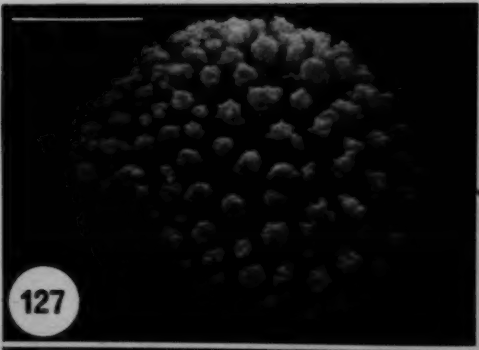
Fig. 127. Scale=10 μm.

Fig. 128. Scale=4 μm.

Figs. 129–130. Proximal surface.

Fig. 129. Scale=10 μm.

Fig. 130. Scale=4 μm.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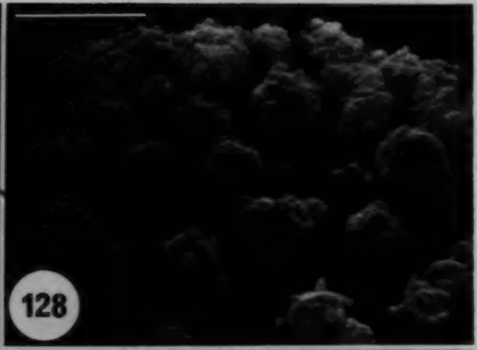
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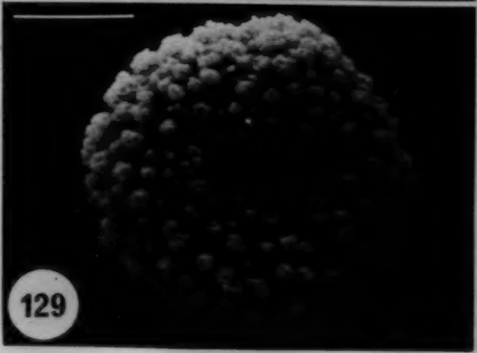
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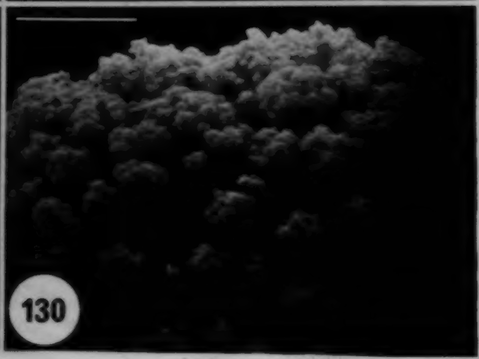
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indistinguishable from those of *E. mutica* and the spores are similarly gemmate with minutely irregular gemmae. However, calyptrae of *E. alpina* are lacerate at the base, rather than fringed, and lack the basal constriction and extension characteristic of *E. mutica*. Also, the leaves of *E. alpina* are narrowly acute and apiculate with the prominent basal cells defined by dark-orange walls that contrast with the yellowish walls of the well-defined marginal border. *Encalypta mutica* is most apt to be confused with *E. microstoma* or *E. vulgaris* and particularly with some forms of *E. rhaptcarpa* with muticous leaves and gymnostomous capsules. *Encalaypta microstoma* can be differentiated by the yellow coloration of the plants, particularly of the capsules, which is quite different from the beige tones that characterize capsules of *E. mutica*. The spores of *E. microstoma* always have a distinct trilete mark on the proximal surface and are heteropolar. When Hagen (1899) described *E. mutica*, he suggested that his species is closely related to *E. vulgaris*, but noted that the two species could be differentiated by a group of character-states. He stated, quite correctly, that *E. mutica* differed in the following ways: "...die Blätter sind stumpfer, die Rippe viel Schwächer, am Rücken sehr dicht papillös, viel einfacher gebaut,...". In contrast, the costa in *E. vulgaris* is very thick and prominent right to the apex of the leaf and is golden-brown and smooth throughout. In transverse section, there are many more layers of stereids. He also noted that the fringed calyptra of *E. mutica* differentiates these two species. In *E. vulgaris* the calyptra is slightly irregular to erose at the base. A greater problem is with the forms of *E. rhaptocarpa* that are quite frequently intermixed. Not only do these converge with *E. mutica* in the general structure of the leaves and the lack of a peristome, but the capsules are not always ribbed and then such plants are almost impossible to distinguish. The only reliable feature to differentiate such plants is the spores. In both *E. vulgaris* and all forms of *E. rhaptocarpa*, the spores are characterized by prominent verrucae on the distal surface, which appear hollow under the light-microscope.

Description: *Plants* to 9 mm tall, light-green to olive-green, brown below, ± branched. *Stem* in transverse section with central strand undifferentiated or indistinct, cells small, walls thin. *Brood bodies* absent. *Axillary hairs* sparse. *Leaves* when dry slightly incurved and slightly twisted, laminae inflexed to conduplicate; 1.2–2.1 mm long, 0.5–0.9 mm wide, oblong, elliptic-oblong, obovate-oblong or lingulate, apex quickly narrowed, muticous; margins plane to reflexed or narrowly recurved along 1 margin, few along both, for short distance from just above basal cells. Costa ends well below apex to subpercurrent, abaxial surface ± keeled, dull to somewhat shiny basipetally, green above to dark-red basipetally, sparsely papillose near base, more densely so distally from just above basal cells, papillae as upper laminal papillae, laminal-type cells cover costa in upper part; in transverse section 2 rows ventral cells, begleiters undifferentiated, 3-4 rows stereids. Upper laminal cells 9-16(18) μm wide, (9)12-18(22) μm long, walls slightly and irregularly thickened, with (2)3-5 papillae per cell, each ± distinctly "c"-shaped; upper marginal cells 14-16 μm wide, 7-9(12) μm long; transitional cells smooth well above basal cells on abaxial surface, on adaxial surface smooth farther above; basal laminal cells 25-75 μm long, 14-23 μm wide, inconspicuous in most, prominent in few, transverse walls pale-orange in most, orange in few, longitudinal walls yellowish, superficial walls smooth, entire to irregularly ± perforated. Goniautoicous. Perichaetial leaves sheath-like and broadly ovate to lingulate below, ± quickly narrowed to acute or obtuse apex; perigonial leaves 0.8 mm long, ± sheath-like and broadly ovate to lingulate below, quickly narrowed to acute apex, few are ligulate and do not sheathe, margins plane; perigonial paraphyses with upper cells entire, walls smooth or with sparse, very low, rounded papillae.

Seta 2-8(10) mm long, erect to flexuose, slightly twisted sinistrorsely below, ± twisted dextrorsely in upper part, shiny and dark-red to orange or blackish; in transverse section 140-150 μm in diameter. Capsule 1.2-2.5 mm long, when dry cylindric and delicately striate, very slightly contracted right at mouth, slightly puckered at base and abruptly contracted to seta, pale-golden to golden-brown with very narrow, shiny, crimson-red rim, when young golden-green with crimson-red rim, when old ± collapsed and indistinctly ± spirally plicate; exothecial cells 45-150 μm long, 12-32 μm wide, in ± regular, longitudinal rows, in transverse section walls slightly and evenly thickened on external surface, 2.3 μm thick; rim cells in (2)3-4 irregular rows, lower cells slightly overlap cells in row above, 12-16 μm wide, 7-18(35) μm long, walls somewhat evenly thickened, dark-orange, uppermost row with walls thin and hyaline; stomata superficial, scattered, 32-41 μm long, 30-37 μm wide. Peristome absent. Operculum 0.5 mm long, plano-convex and rostrate. Annulus undifferentiated. Spores dark-brown, paraisopolar, in polar view radially symmetric and circular, 25-29 μm, in equatorial view polarly asymmetric and concave-convex, 25-29 μm X 20 μm, ± densely, irregularly gemmate, gemmae very small to moderate sized (ca. 1.0-2.3 μm in diameter), rounded, minutely irregular with SEM. Calyptra 1.8-4.0 mm, cylindric to elliptic-cylindric, very distinctly contracted to slightly curved or erect rostrum that is (0.5)0.8-1.0 mm long, cylinder perfectly smooth and turgid to faintly puckered, slightly constricted at base and narrowly ± extended horizontally to obliquely, fringed, segments ± regular, narrowly trapezoidal, 0.2 mm long, incurved to pendent to slightly expanded, ± broken off, calyptra golden to dark-brown distally with brownish to white fringe, shiny, ± transluscent, smooth; in transverse section cylinder with 2-3 layers of cells with very thick walls, fringe with 1 row of cells, walls very strongly thickened; in superficial view fringe cells short to long-oblong. Chromsome number n=12 (Horton 1979a).

Habitat: In North America, most populations of E. mutica occur in the main ranges of the Rocky Mountains; however, a few more-or-less disjunct populations have been collected east of the Mountains in boreal and subarctic regions. In the mountains, E. mutica is to be found from the lowest elevations in the valleys up into the alpine zone. At lower elevations in southwestern Alberta, some populations are associated with rushing streams where they occur on exposed soil in more-or-less shaded, mesic habitats, many with a northerly aspect. In this general area also, other populations are found in more exposed habitats, on soil churned by needle-ice action in roadside ditches or on open, treeless knolls. Throughout the Mountains, E. mutica characteristically occurs on rock outcrops on exposed ledges where small piles of soil have accumulated as a result of slippage. Plants are seldom found in crevices of rock outcrops. In northerly areas of the Rocky Mountains in British Columbia, the Yukon and Northwest Territories, and Alaska, populations of E. mutica also occur on exposed, drier soil of talus slopes. Two of the collections of E. mutica from extramontane localities, in the Ft. Simpson area of the Northwest Territories and the Ft. McMurray area of Alberta, were on rock outcrops associated with streams or rivers. The third, from the Mackenzie Delta area, was found on exposed soil at the base of an uprooted tree. Therefore, this species appears to have a rather broad range of tolerance with respect to exposure and moisture conditions. Such associates as *Ditrichum flexicaule* (Schwaegr.) Hampe, *E. longicolla*, *E. procera*, *Fissidens arcticus* Bryhn and *Myurella sibirica* (C. Müll.) Reim. are indicative of more mesic habitats, while *Bryoerythrophyllum recurvirostrum* (Hedw.) Chen, *Bryum wrightii* Sull. *et* Lesq., *E. rhaptocarpa*, *Plagiobryum demissum* (Hook.) Lindb., *P. zierii* (Hedw.) Lindb., *Stegonia latifolia* (Schwaegr. *ex* Schultes) Vent *ex* Broth. var. *latifolia*, *S. latifolia* var. *pilifera* (Brid.) Broth., *Tortula mucronifolia* Schwaegr., *Tortella fragilis* (Drumm.) Limpr. and *T. tortuosa* (Hedw.) Limpr. are generally associated with more exposed, drier habitats.

In Scandinavia, *E. mutica* is restricted to montane habitats, and the frequent association of *Ditrichum flexicaule*, *Myurella julacea* (Schwaegr.) B.S.G. and *Stegonia latifolia* var. *pilifera* suggest habitat preferences similar to those of the North American populations. This supposition is borne out, at least in part, by Tuomikoski's (1939) report that *E. mutica* occurs "...auf Felsen auf nackter Erde, doch nicht in engeren Spalten o.dgl.auf, wie dies bei mehreren anderen Arten der Fall ist...".

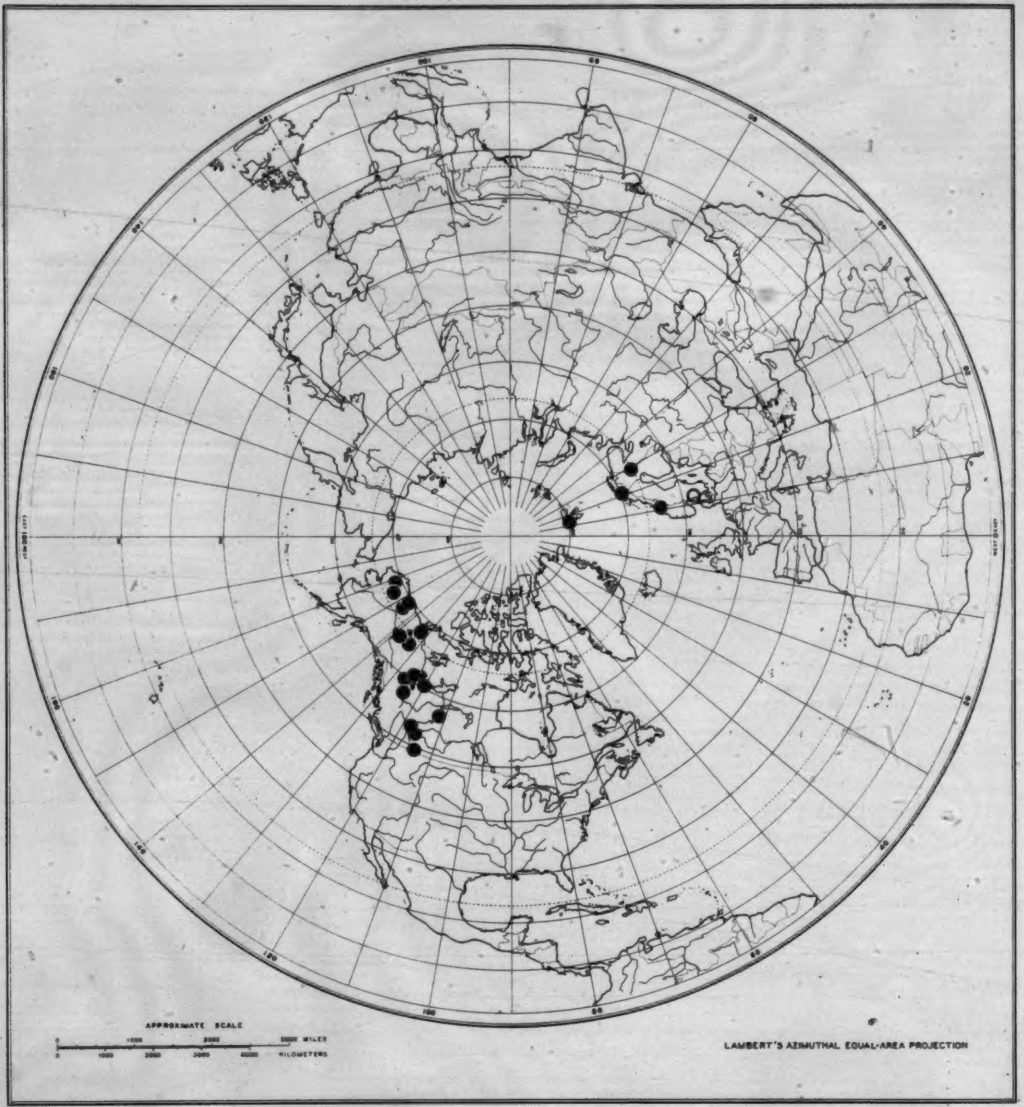
The substrate-type is probably of crucial importance in determining the occurrence of *E. mutica* (Horton 1979a). In North America, pH of the soil on which populations were growing ranged from 7.1 to 7.8 (n=40 from 24 different localities) with a mean of 7.4 (s.d.=±0.2) (Fig. 300). Concentrations of Ca^{++} and Mg^{++} in the soil are also high relative to other species of *Encalypta* (Figs. 301–302, Table 9). Hagen (1910) stated that populations of *E. mutica* in Norway are restricted to "...Schiefer- und Kalkgebiete...", and when Tuomikoski (1935) reported *E. mutica* new to Finland, he noted that this population was growing on calcareous rocks. Virtually all of the species commonly associated with *E. mutica*, cited above, reflect this restriction to calcareous substrates. Characteristically, the soil on which populations of *E. mutica* are found growing is mineral with a very low humus content.

Distribution: *Encalypta mutica* is reported from western North America, Svalbard and Scandinavia (Fig. 131). In North America, *E. mutica* is known only from the Western Cordillera and a few slightly disjunct localities just east of the mountains. It is reported from Alaska in the Brooks Range; from the Yukon Territory in the Ogilvie, southern Richardson and Wernecke Mountains; from the western Northwest Territories in the

Figure 131. Distribution of *Encalypta* *mutica*.

WORLD, NORTHERN HEMISPHERE

No. 201PN


APPROXIMATE SCALE
0 1000 2000 MILES
0 1000 2000 3000 4000 KILOMETERS
LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION

GOODE'S SERIES OF BASE MAPS
HENRY M. LEPPARD, EDITOR

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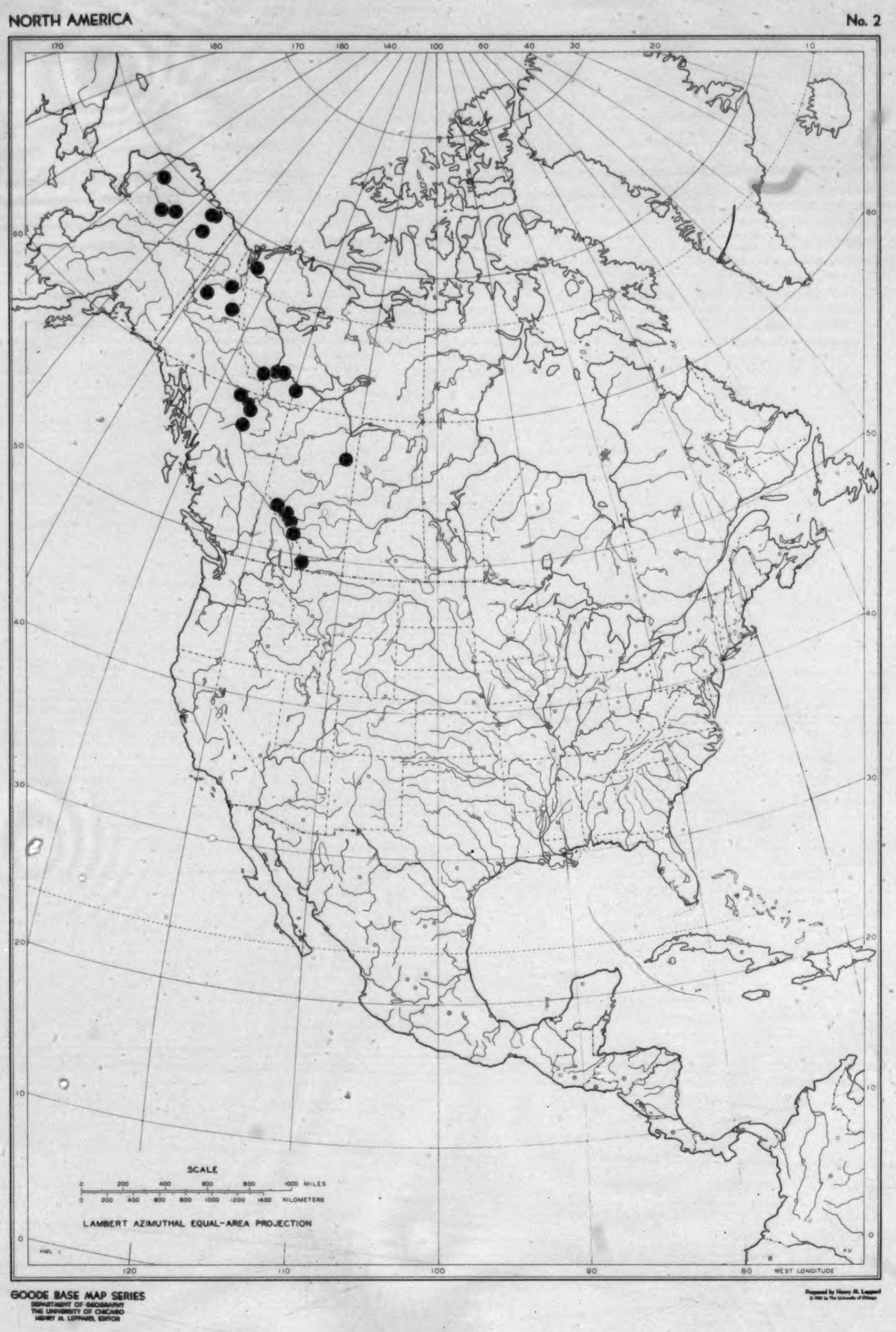
Mackenzie Delta, the Nahanni Range of the Mackenzie Mountains and Whittaker Falls in the Fort Simpson area; from northcentral British Columbia in the Rocky Mountains; from Alberta in the Rocky Mountains and a disjunct locality in the Fort McMurray area (Fig. 132). In Scandinavia, *E. mutica* is known from a few localities in Norway, Sweden and Finland. In Norway, it is reported from Finmark, Nordland and Sör-Tröndelag; in Sweden, it has been reported from Västergötland (Tuomikoski 1939) (indicated on map with an open circle); and in Finland, *E. mutica* is reported from Kuusamo (Fig. 133). Tuomikoski (1939) reported it also from Lapponia enontekiensis in Finland citing specimens from Saana and Toskalharji collected by Roivainen. However, I have been able to trace only one of these specimens and this one (*Roivainen* 24.7.1935 - H) from Toskalharji is not *E. mutica*, but a form of *E. rhaptocarpa*. Two further specimens from the same locality, collected by Roivainen in 1955, are determined as *E. mutica*, but both are sterile populations of a pottiaceous taxon. Therefore, it appears that the records of *E. mutica* from Lapponia enontekiensis are doubtful.

Nowhere within its range can *E. mutica* be considered a common species. In North America, "...*E. mutica* rarely occurs in extensive tufts, but sporadic populations of a few plants are quite frequent when the substrate is distinctly calcareous." (Horton 1979a). By comparison to another strict calciphile, *E. longicolla*, *E. mutica* is of more frequent occurrence in the southern Canadian Rocky Mountains in southwestern Alberta, but farther noth both are found with more-or-less equal frequency. In Scandinavia, Hagen (1910) reported *E. mutica* to be more frequent in the northern part of Norway; it appears to be very rare in Sweden and Finland.

Phylogenetic Relationships: *Encalypta mutica* seems quite isolated from other species of *Encalypta* with few characteristics that suggest even a distant relationship with another species. The paraisopolar spores with minutely irregular gemmae are most like those of *E. alpina* and capsules in some populations of *E. mutica* are also very similar to those of *E. alpina*. Overall, the coloration of plants of *E. mutica*, the rich green leaves, red to blackish seta and pale brown capsule, is not unlike that of *E. alpina*. Otherwise, there is little resemblance between these two species, so the significance of spore and capsule structure is difficult to assess.

Figure 132. Distribution of *Encalypta mutica* in North America.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LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
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110
100
90
80
WEST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR
Prepared by Henry M. Leppard
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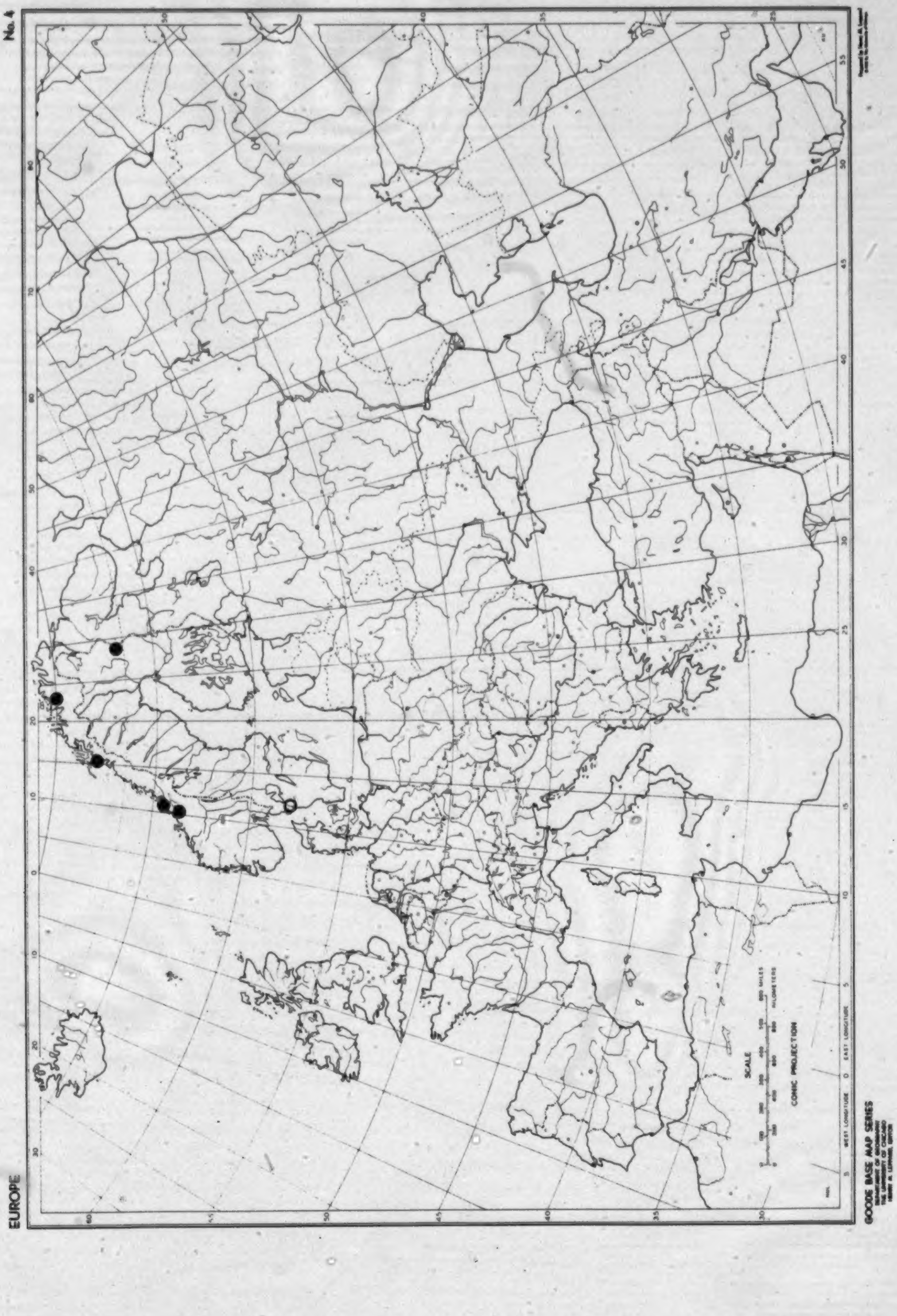
Figure 133. Distribution of *Encalypta mutica* in Europe.


EUROPE
No. 4
SCALE
MILES
KILOMETERS
CONIC PROJECTION
WEST LONGITUDE
EAST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
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Specimens Examined: ALA (11), ALTA (70), CANM (4), H (12), Priv. Herb. D. G. Horton (40), JE (2), NY (4), O (7), S (1), TRH (7).

ENCALYPTA AFFINIS Hedwig f.

Beitr. Naturk. 1: 121, pl. 4, figs. 1-6. 1806.

Figs. 30-31,134-156.

Type: "Helvetiae indigenam misit amicissimus Schleicher hanc Encalyptam, quae locum natalem immixta sibi Jungermannia..." (Lectotype: "Encalypta affinis Hedw. fil. in Mohr & Web. Beytr. Z Naturkunde beschrieb." LAU-Schleicher (in part)!; Isotypes: LAU-Schleicher (in part)!).

Nomenclatural Notes: The two potential type specimens of *E. affinis* in Hedwig's herbarium both consist of only *E. alpina*, which was described earlier by Smith (1805). However, it is clear that the original description and illustrations of *E. affinis* were, at least in part, based upon plants of what is currently known as *E. affinis*. This taxonomic concept of *E. affinis* is well established historically and the epithet *affinis* has been fairly consistently applied, particularly recently. It seems significant that the specimen in Schleicher's (cited by Hedwig (1806) as the collector) herbarium, the label information of which corresponds to that in Hedwig's herbarium, consists of both *E. alpina* and the taxon presently referred to as *E. affinis*. Therefore, I have concluded that the specimen in Hedwig's herbarium did, when the description of *E. affinis* was prepared, contain plants of this taxon, in addition to the plants of *E. alpina* that remain there presently. I feel that it is important to maintain continuity between the epithet and the taxonomic concept that has been associated with that name, if possible within the rules of the ICBN (Stafleu *et al.* 1978). In consideration of the circumstances outlined above, I selected a lectotype for *E. affinis* in the collector's herbarium and did not consider the specimens in Hedwig's herbarium to be part of the type; for further details, see Horton (1981b).

Diagnosis and Differentiation: The dark-brown tones that characterize the plants of *E. affinis* are one of the most distinctive features of this species. Only the uppermost leaves are light-green and even these, in many populations, have dark-brown apices, and the other leaves are characteristically dark-brownish olive-green to dark-brown. Encalypta affinis is also defined by an opaque, papillose calyptra with the long rostrum indistinctly contracted from the long, narrow cylinder. The cylinder is always delicately puckered and there is generally a slight constriction at the base just above the short, irregular fringe, the segments of which are more-or-less broken off once exposed. Also characteristic is the long, narrowly cylindric capsule with a more-or-less distinctly differentiated, short neck. The capsule is pale-golden with a bright-red rim and is delicately puckered like the calyptra. While the peristome appears to consist of a single layer of teeth, there are actually two, but these are almost completely fused. The relatively long, linear peristome teeth are a distinctive pink color and densely papillose. The moderately long seta is dark-red below and orange to yellowish distally. Leaves are long and narrowly oblong with the margins narrowly to broadly recurved basipetally from near or well below the narrowing of the apex. The leaf apex is either hair-pointed (see E. affinis subsp. affinis) or muticous (see E. affinis subsp. macounii). The green to dark-brown costa forms a relatively prominent keel and is densely papillose in the lower part so that it appears dull under the stereoscope. Overall, from the shape of the calyptra, capsule and leaves, one is left with an impression of length and narrowness in E. affinis. Important microscopic features of E. affinis include the dark-orange transverse walls of the basal leaf cells and the dense, well-developed papillae restricted to the abaxial surface of these cells. Also, the basal marginal cells are colored orange as the laminal cells and even more densely papillose on the abaxial surface than the laminal cells. In transverse section, the costa has a well-developed band of five or six rows of stereids. The orange spores are relatively small and more-or-less regularly gemmate, the gemmae small and clearly defined.

Encalypta affinis might be confused with several closely related species, including E. brevicolla, E. ciliata and E. procera. The calyptra of E. brevicolla is virtually indistinguishable from that of E. affinis, except that the rostrum is somewhat more distinctly contracted from the cylinder in E. brevicolla. Plants of E. brevicolla are more readily differentiated by the broader capsule that is crimson-red in the upper part, the white peristome, leaves with plane margins and a long hair-point, and the blackish rather

Figures 134-139. **Encalypta affinis.** Scale=1 mm.

Fig. 134. Calyptrae.

Fig. 135. Capsules.

Figs. 136-137. *E. affinis* subsp. *macounii*.

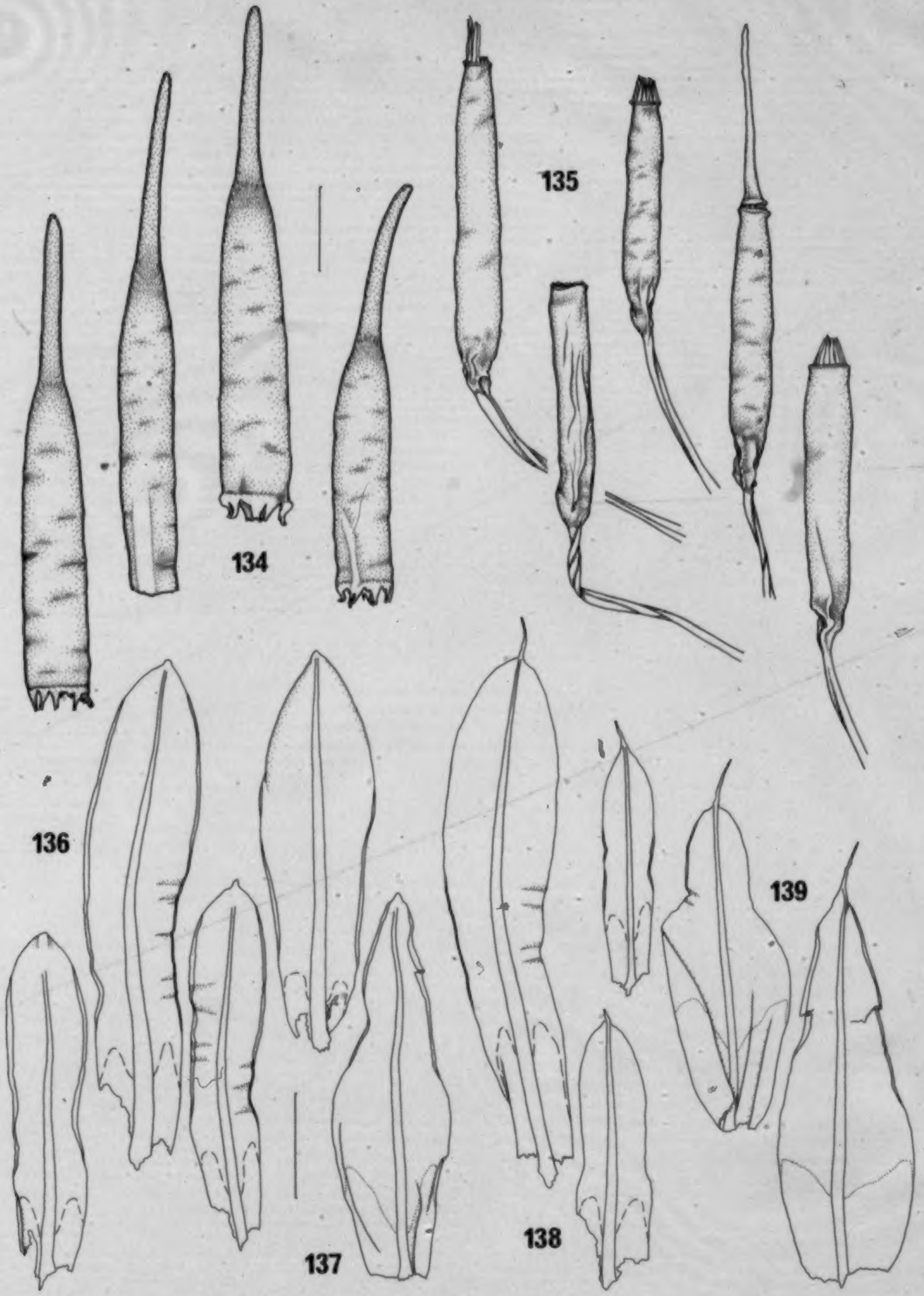
Fig. 136. Vegetative leaves.

Fig. 137. Perichaetial leaves.

Figs. 138-139. *E. affinis* subsp. *affinis*.

Fig. 138. Vegetative leaves.

Fig. 139. Perichaetial leaves.



Figures 140-145. Variation in Spores of *Encalypta affinis*.

Figs. 140–143. Distal surface.

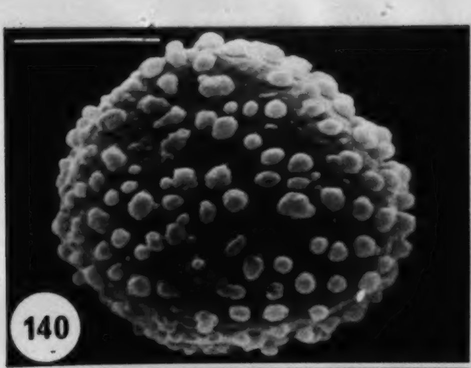
Fig. 140. Scale=10 m.

Fig. 141. Scale=4 m.

Fig. 142. Scale=10 m.

Fig. 143. Scale=2 m.

Figs. 144–145. Proximal surface. Scale=10 m.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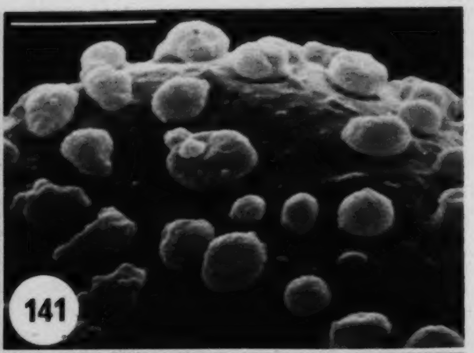
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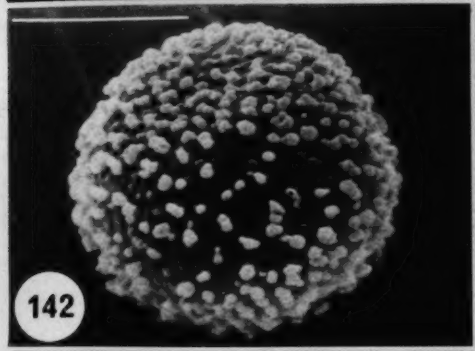
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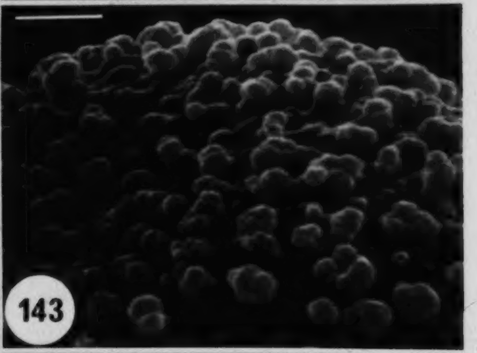
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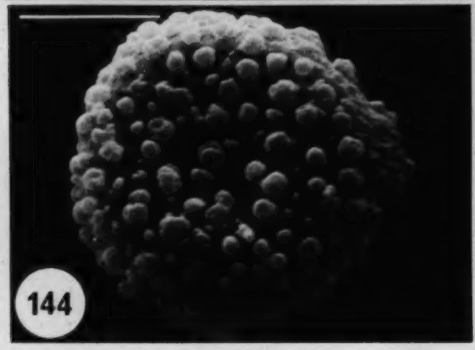
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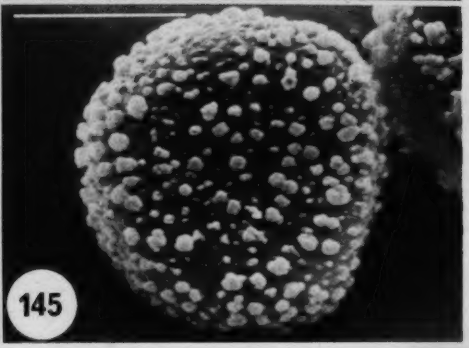

145

Figures 146-149. **Encalypta affinis.**

Figs. 146-148. Variation in Spores (cont'd).

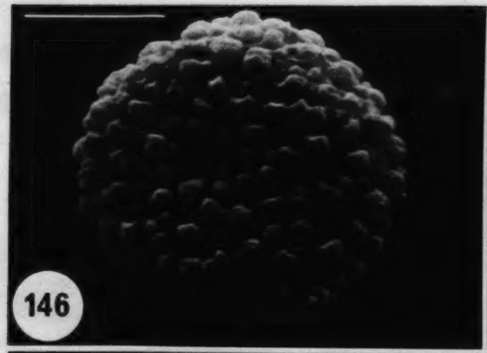
Figs. 146-147. Proximal Face.

Fig. 146. Scale=10 m.

Fig. 147. Scale=4 m.

Fig. 148. Distal Face. Scale=10 m.

Fig. 149. Basal Leaf Cells with smooth walls on adaxial surface and papillose walls on abaxial. Scale=100 m.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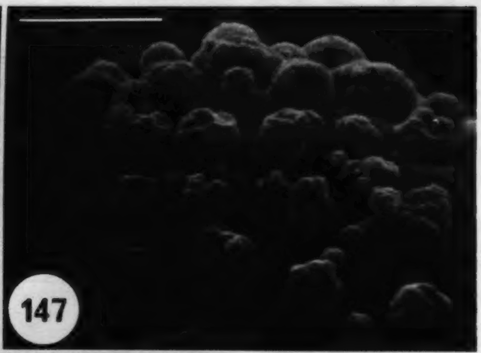
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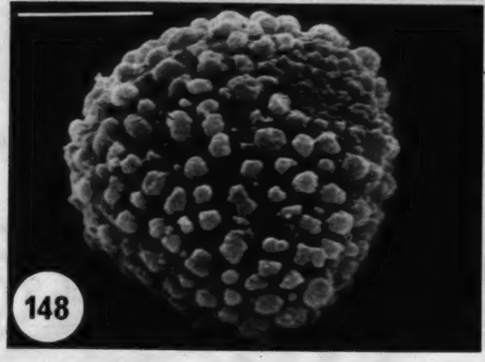
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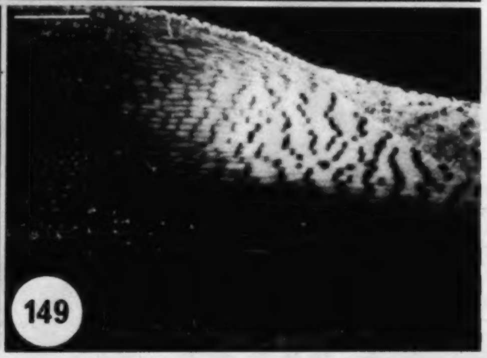
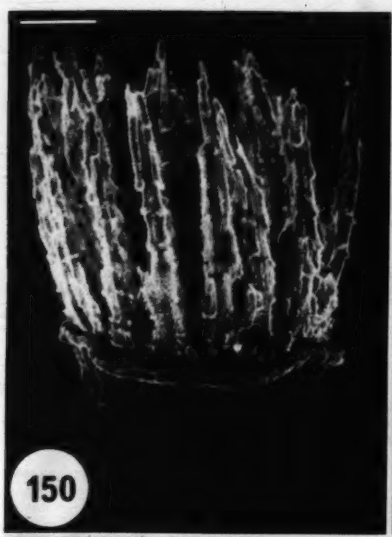

149

Figures 150-153. Peristome of *Encalypta affinis*.

Figs. 150-151. Scale=100 m.

Fig. 152. Outer surface with vertical division on each tooth. Scale=50 m.

Fig. 153. Inner surface with vertical division at base of each tooth. Scale=50 m.



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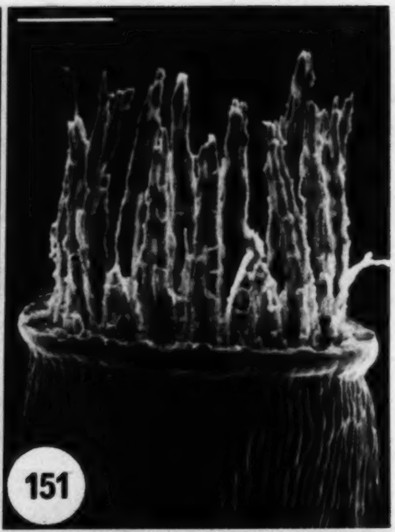

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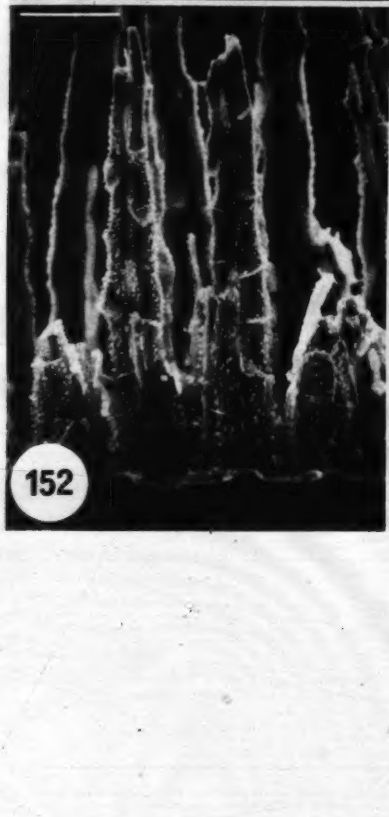

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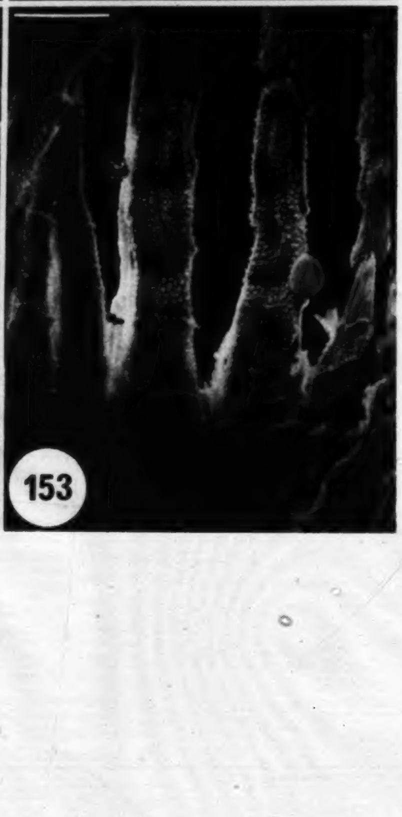

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than brown overtones in the coloration of the leaves. Microscopically, E. brevicolla has a distinct basal marginal border of pale green cells and the walls of the basal cells are smooth on both surfaces. In transverse section there are only two to three rows of stereids in the costa and the larger spores are characterized by large, gemmate protuberances.

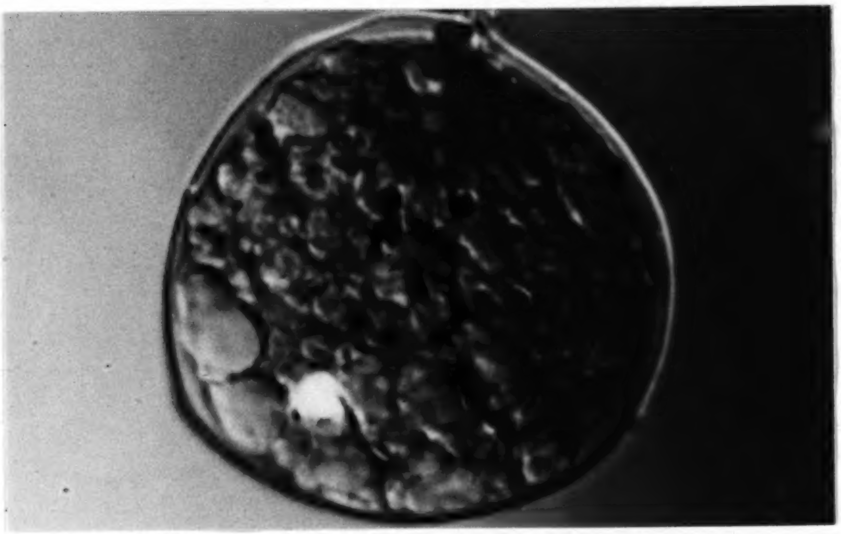
Encalypta ciliata can be differentiated from E. affinis by the rich, yellow tones that characterize the calyptra, capsule, seta and leaves. Structural differences include the shorter cylinder of the calyptra, which is very distinctly narrowed to the rostrum. At the base there is a narrow, but distinct, horizontal extension from which the precisely segmented fringe is pendent. The perfectly smooth capsule is distinctly constricted just below the mouth and the peristome teeth are lanceolate. Leaves are broader and there is a prominent costa that is smooth and shiny. Microscopically, E. ciliata, like E. brevicolla, is characterized by leaves with a basal marginal border and smooth basal cells; two to three rows of stereids in the transverse section of the costa; and larger spores with a distinct trilete mark on the proximal surface. See Diagnosis and Differentiation under E. affinis subsp. affinis and E. affinis subsp. macounii for discussions of the features that differentiate E. procera from each of these taxa.

Description: Plants to 30 mm tall, light-green to brownish olive-green to dark-brown above in most populations, fewer with blackish tones, brown below, ± branched. Stem in transverse section with central strand undifferentiated. Brood bodies absent. Axillary hairs abundant, in rows of up to 12 filaments joined laterally below, covered by gelatinous substance, up to 2 mm long, hyaline, thin-walled, unbranched, attached to leaf bases and stem. Leaves when dry incurved and irregularly ± twisted, laminae inflexed to conduplicate, apex ± cucullate; (2.2)3.5–5.5(6.5) mm long, 0.7–1.0(1.2) mm wide, narrowly-oblong to oblong, with slight constriction just above basal cells in most populations, fewer narrowly-obovate, apex dark-brown in many populations except in uppermost leaves, quickly narrowed in most populations, fewer gradually or abruptly narrowed, muticous to broadly mucronate or apiculate to short hair-pointed; margins slightly irregularly and narrowly to broadly recurved from narrowing of apex or below to just above basal cells, in very few populations plane or almost so. Costa ends well below apex to excurrent, abaxial surface inconspicuously keeled above, relatively dull to slightly shiny above, dull basipetally, green to dark-brown in virtually all populations, distinctly reddish in 1 population, very densely papillose almost from base, papillae very large and much branched with long branches, many "o"-shaped, ± papillose distally, papillae low and rounded, when costa ends below apex papillose laminal-type cells cover upper part; in transverse section with 2-3 rows of ventral cells, begleiters undifferentiated, 5-6 rows of stereids. Upper laminal cells (9)12-14(16) μm wide, (9)14-16(20) μm long, with 2-4 papillae per cell; upper marginal cells 9-12(14) μm wide, 9(12) μm long; transitional cells densely papillose to basal cells on abaxial surface, papillae large and much-branched with long branches, some "o"-shaped, on adaxial surface smooth somewhat above basal cells; basal laminal cells 35-105 μm long, 7-18 μm wide, prominent, transverse walls orange, longitudinal walls hyaline, abaxial walls mostly entire, some irregularly perforated, papillose above to ± smooth near leaf base, most papillae associated with transverse walls, adaxial walls smooth, mostly entire, some irregularly perforated; basal marginal cells ± undifferentiated, strongly papillose almost to leaf base. Goniautoicous. Perichaetial leaves slightly longer than vegetative leaves in most plants, narrowly oblong above ± broadly ovate sheath-like base, apex broadly, few narrowly, acute; perigonial leaves 1.1-1.2 mm long, broadly ovate and sheath-like below, quickly narrowed to muticous or apiculate apex; perigonial paraphyses with walls smooth, few with low papillae.

Seta 6-16 mm long, flexuose in most populations to erect, ridged and slightly twisted sinistrorsely below, ± twisted dextrorsely near capsule, shiny and dark-red below, orange, pale orange or yellowish in upper part, dull orange with age; in transverse section 160-185 μm in diameter below. Capsule (2.0)2.5-4.0 mm long, when dry narrowly cylindric to cylindric with slight constriction just below slightly irregular and oblique mouth, slightly constricted basally, then narrowed to seta through puckered neck, in some neck is collapsed and indistinct, most are delicately puckered throughout, few are perfectly smooth, pale golden with bright-red rim, when young greenish pale-golden with bright-red rim, when old ± collapsed and longitudinally striate, dull-orange; exothecial cells 50-130 μm long, 14-35 μm wide, in longitudinal rows, in transverse section walls evenly thickened on external surface, 4.0-4.5 μm thick; rim cells in 2-4 irregular rows, 12-20 μm wide, 9-28 μm long, walls slightly, evenly thickened; stomata superficial, 4–8, restricted to capsule base above neck, 44–46 µm long, 35–37 µm wide. Peristome (0.3)0.4–0.6 mm long, in 2 concentric layers, exostome teeth and endostome segments almost completely fused, 16, erect to slightly incurved, lanceolate-linear, some ± longitudinally fenestrate, pink, exostome outer surface with 2 vertical rows of cell plates, densely irregularly papillose, inner surface with trabeculae fused to endostome, endostome ± joined basally by very low basal membrane that extends to or only slightly above capsule rim, inner surface with 2 vertical rows of cell plates basally, densely irregularly papillose; preperistome absent. Operculum narrowly conic and long-rostrate, 2.0–2.2 mm long. Annulus undifferentiated. Spores orange, paraisopolar, in polar view radially symmetric and circular, (20)23–25(28) µm, in equatorial view polarly asymmetric and concave-convex, (20)23–25(28) µm X 16 µm, ± regularly gemmate, gemmae small to moderately sized, 1.5–2.3 µm in diameter, rounded to elongate and somewhat irregular, exospore surface smooth between gemmae. Calyptra (4.5)5.5–7.0(8.0) mm long, extends well below capsule, long and cylindric to narrowly-cylindric, indistinctly contracted to slightly curved or erect, long rostrum that is 1.8–2.4 mm long, cylinder slightly and distinctly constricted at base in most populations, some lack constriction, some with slight horizontal or oblique expansion, fringed, segments rather irregularly trapezoidal, 0.2–0.3 mm long, pendent, slightly incurved to slightly flared, ± broken off in most, calyptra golden to golden-brown distally with brownish to white fringe, dull to slightly shiny, opaque, ± strongly papillose, papillae tend to be larger and more sharply pointed in rostrum in most; in transverse section cylinder with 3 rows of cells with small lumina and very thick walls; fringe with 1 row of cells, walls exceptionally thickened in 2 layers, outer yellowish, inner hyaline; in superficial view fringe cells short- to long-oblong with 2–4 irregular rows of quadrate cells at juncture with cylinder. Chromosome number n=13 (Anderson & Crum 1958), (Fig. 154).

Variation: Encalypta affinis is a clearly defined species and is relatively uniform throughout its range in the character-states described under Diagnosis and Differentiation, except in the structure of the leaf apex and the costa. In these features, populations can be separated into two groups, with one characterized by muticous leaves or a very broadly mucronate apex and a costa ending well below the apex or

Figure 154. *Encalypta* *affinis* - Chromosome Number n=13.



subpercurrent (Figs. 136-137), and the other by apiculate or short hair-pointed leaves and an excurrent costa (Figs. 138-139). Also, there is a general tendency for populations with muticous or broadly mucronate leaves to have broadly recurved margins and for those with apiculate or short hair-pointed leaves to have very narrowly recurved margins, but these are not consistent correlations. features. Limpricht (1890) described the leaves of E. affinis as "stumpf oder kurz zugespitzt,..."; however, further on in the description, he emphasized that the costa is "...in eine längere oder kurzere Stachelspitze austretend,...", so it is possible that his description of obtuse leaves referred to ones with the hair-point broken off. Coker (1918) quite clearly was aware of the two different leaf-types that occur in E. affinis. She noted that "The American specimens of this species seem to have the leaves more often blunt than is usual in the European ones,...", but she considered both forms within her concept of E. affinis.

With the advantage of having more specimens from both North America and Eurasia available to me for study than Coker had, I have found that these structural differences between different populations of E. affinis do not occur randomly. In western North America, populations with the costa ending below the apex occur throughout the range of this species southward from southern Alaska, the central and eastern Yukon Territory, and the extreme west-central Northwest Territories. The populations with an excurrent costa are restricted to northern Alaska, the Yukon and Northwest Territories, and Greenland. In the central Yukon and Northwest Territories, the two forms occur together at some localities, but as yet I have not found them growing intermixed. In Eurasia the distribution patterns are just the reverse. Populations with an excurrent costa occur throughout mountainous regions of central and northern Europe, and central and northern Asia, and there are only a few, sporadic populations with muticous leaves in Fennoscandia. Therefore, for the most part, North American populations of E. affinis are characterized by muticous leaves and those in Eurasia by hair-pointed leaves. In conclusion, there is a structural difference between populations of E. affinis in two character-states (however, these might be genetically linked), and this difference is correlated with geographical isolation of these populations. Therefore, I feel that these differences should be given taxonomic recognition at the level of subspecies (see Taxonomic Concepts under Material and Methods).

ENCALYPTA AFFINIS Hedwig f. subsp. AFFINIS

Figs. 138–139.

Encalypta capillata Schkuhr, Deutschl. Krypt. Gew. 2(2): 46. 1811. *Nom. illeg. incl. spec. prior.*

Encalypta pilosa Röhl., Deutschl. Krypt. Fl. ed. 2, 3: 53. 1813. *Nom. illeg. incl. spec. prior.*

Encalypta apophysata Nees, Hornsch. *et* Sturm, Bryol. Germ. 2(1): 49, pl. 15, fig. 5. 1827. *Nom. illeg. incl. spec. prior.*

Encalypta cylindrica Funck *ex* Nees, Hornsch. *et* Sturm, Bryol. Germ. 2(1): 52, pl. 15, fig. 6. 1827. Type: "...Sommer 1825 von Herrn *Funck* im Witschthal in Tyrol..." (Lectotype: "Encalypta cylindrica Witschthal [illegible] Funk. 1826" B-Brid.!; Isotype: FI!; Possible Isotypes: BM-Schimp.!, S-Möll.!).

Encalypta cylindrica Funck *ex* Brid., Bryol. Univ. Suppl. I: 767. 1827. Type: "In Witschthal, Alpinum Tyrolensium caespitose habitat. Clar. Funckius detector communicavit." (Lectotype: based on same type as *E. cylindrica* Funck *ex* Nees, Hornsch. *et* Sturm, B-Brid.!).

Encalypta fimbriata Lam. *et* DC. var. *elongata* Brid., Bryol. Univ. Suppl. I: 767. 1827. Type: "Prope St. Gertrud in Martell-thal Tyrolis. Funck." (Holotype: "Encalypta fimbriata var. elongata Encalypta elongata bei St. Gertrud in Martell (Funck 1826)" B-Brid.!).

Encalypta elongata Funck *ex* Brid., Bryol. Univ. Suppl. I: 767. 1827. *Nom. inval. in synon.*

Encalypta ciliata Hedw. var. *elongata* (Brid.) Hüb., Musc. Germ. 106. 1833.

Encalypta ciliata Hedw. subsp. *cylindrica* (Funck *ex* Nees, Hornsch. *et* Sturm) Hampe, Flora 20: 281. 1837.

Encalypta apophysata Nees, Hornsch. *et* Sturm var. *cylindrica* (Funck *ex* Nees, Hornsch. *et* Sturm) Rabenh., Deutschl. Krypt. Fl. 2(3): 171. 1848.

Leersia affinis (Hedw. *f.*) Lindb., Musc. Scand. 20. 1879. *Nom. inval.*

Diagnosis and Differentiation: *Encalypta affinis* subsp. *affinis* was described from a specimen collected in Europe, probably in the Swiss Alps. The plants in this specimen have leaves with an excurrent costa. Therefore, *E. affinis* subsp. *affinis* is characterized by vegetative, perichaetial and perigonial leaves that are apiculate to short hair-pointed with the costa excurrent. There is also a tendency for the margins of the leaves to be narrowly, rather than broadly, recurved. In all other respects this subspecies has the features of the species as a whole (see Diagnosis and Differentiation, and Description of E. affinis).

Plants of E. procera with sporophytes are particularly difficult to differentiate from those of E. affinis subsp. affinis, which they resemble in the short hair-pointed leaves with recurved margins. Encalypta procera can be distinguished by the shorter rostrum of the calyptra, the spirally twisted capsules and the long, clearly double peristome with the two layers of teeth separate in the upper part. The basal cell walls of the leaves are smooth; and both the longitudinal and transverse walls are dark-orange.

ENCALYPTA AFFINIS Hedwig f. subsp. MACOUNII (Austin) Horton

Comb. et Stat. Nov.

Figs. 136-137.

Basionym: Encalypta macounii Austin, Bot. Gaz. (Crawfordsville) 2: 97. 1877. Type: "Stewart's Lake Mountains, June, 1875, Macoun." (Lectotype: "Encalypta macouni Stewart's Lake Mountains, June 21/75 Macoun." NY-Austin!; Isotypes: BM!, NY (2 specimens)!).

Encalypta leiocarpa Kindb. in Mac., Bull. Torrey Bot. Cl. 17: 273. 1890. Type: "On rocks summit of Mount Queest and other mountains in the Gold Range, B.C. Alt. 6,500 feet. August 8, 1889." (Lectotype: "Encalypta leiocarpa Kindb. n. sp. N. Amer., Brit. Columbia, Mt. Queest, Gold Range 6500 f. 24/7 89 J. Macoun" S-Kindb.!; Isotypes: BM-Kindb.!, CANM!, NY (3 specimens)!).

Nomenclatural Notes: Austin (1877) was the first to describe plants of E. affinis with muticous leaves as E. macounii, based upon a specimen collected by John Macoun in British Columbia. Later, Kindberg (1890) also described such plants as E. leiocarpa. However, it is questionable whether Kindberg really understood the structure of the plants he was describing in relation to other species in the genus Encalypta, as he differentiated his new species from E. streptocarpa and made no mention of E. affinis. In contrast, Austin compared his *E. macounii* to *E. affinis* and correctly differentiated it on the basis of the muticous leaves and the costa ending below the apex, although he also cited other differences that I have been unable to substantiate. Considering that Austin had a good understanding of the relationships of the taxon that he was describing according to present taxonomic concepts, I have chosen to designate the subspecies of *E. affinis* with muticous leaves as *E. affinis* subsp. *macounii*. It seems fitting that John Macoun, who did so much to permanently record the moss flora of western Canada, should have his name commemorated in a genus of which he collected many specimens. However, it is perhaps also a little ironic, but very typical, that Macoun's rather disorganized manner of dealing with specimens led to confusion as to the real identity of *E. macounii*.

In the Catalogue of Canadian Plants, Kindberg (*In* Macoun & Kindberg 1892) reported that he had received original specimens of *E. macounii* from Macoun and stated that Austin's original description was clearly wrong in several critical features. Kindberg concluded that *E. macounii* is actually very closely related to *E. ciliata*. Among the specimens cited under *E. macounii* in the Catalogue of Canadian Plants is one collected in the Great Lakes region by Elizabeth Gertrude Britton, which she had determined as *E. ciliata*. Possibly the suggestion that she had misdetermined this collection motivated Britton and in 1895 she published a rather lengthy review of the conflicting information on *E. macounii*. Britton pointed out that she had examined the specimen of *E. macounii* in Austin's herbarium and that the original description was quite correct in all except one minor aspect. She also maintained that her deterination of the specimen from eastern Canada as *E. ciliata* was equally correct, and questioned the identity of another specimen cited by Macoun and Kindberg (1892) as *E. macounii*. Britton concluded that the so-called original specimens of *E. macounii* that Kindberg received from Macoun are not the same species as that described by Austin. In Kindberg's herbarium (S!), there is a specimen with the following information: "Specimen originale! Encalypta macounii Aust. Canada J. Macoun 1887 determ. Austin". Not only is the date of collection wrong (the type of *E. macounii* was collected in 1875), but the specimen is definitely *E. ciliata*, as are all other purported specimens of *E. macounii* in the Kindberg herbarium. Therefore, Britton (1895) was correct, both in her determination of the specimen of *E. ciliata* (CANM!) and in her conclusion that Kindberg had not been sent material of the same species that Austin described as E. macounii. Other problems that have resulted from John Macoun's unreliable collecting and packeting techniques are reported in Godfrey (1977) and Horton and Schofield (1977).

Diagnosis and Differentiation: Diagnostic of E. affinis subsp. macounii are vegetative, perichaetial and perigonial leaves that are muticous to broadly mucronate with the costa ending well below the apex to subpercurrent. The margins of the leaves tend to be broadly, rather than narrowly, recurved. In all other respects, this subspecies has the characteristics of the species as a whole (see Diagnosis and Differentiation, and Description of E. affinis).

Sterile plants of E. procera are characterized by muticous leaves. Therefore, there is a superficial resemblance to E. affinis subsp. macounii. Encalypta procera is best differentiated by the basal leaf cells with smooth walls. Also, in many populations of E. procera, the prominent clusters of dark-brown brood bodies that occur in the leaf axils are a distinctive feature that immediately circumscribe this species.

Habitat: Snow-release time may be an important factor determining the occurrence of E. affinis. In the montane, through the subalpine into the alpine zone, E. affinis characteristically grows in rather protected habitats where snow-melt is somewhat delayed. Therefore, it is more common on slopes or outcrops with a northerly aspect. In such places, populations grow on soil on the edge of small solifluction terraces or on ledges of rock outcrops with a variety of associated species including Bartramia ithyphylla Brid., Blepharostoma trichophyllum (L.) Dum., Bryum spp., Cladonia pyxidata (L.) Hoffm., Dicranum scoparium (Hedw.) B.S.G., Ditrichum flexicaule (Schwaegr.) Hampe, Drepanocladus uncinatus (Hedw.) Warnst., Eurhynchium pulchellum (Hedw.) Jenn., Hylocomium splendens (Hedw.) B.S.G., Isopterygium pulchellum (Hedw.) Jaeg. et Sauerb., Lophozia barbata (Schmid.) Dum., L. lycopodioides (Wallr.) Cogn., Mnium thomsonii Schimp., Myurella julacea (Schwaegr.) B.S.G., M. tenerrima (Brid.) Lindb., Peltigera horizontalis (Huds.) Baumg., Pohlia cruda (Hedw.) Lindb., Polytrichum juniperinum Hedw., Solorina spp. (but not including S. crocea (L.) Ach.), Timmia austriaca Hedw., Tortella

tortuosa (Hedw.) Limpr. and *Tortula norvegica* (Web.) Wahlenb. *ex* Lindb. Virtually all of these species are characteristically associated with rather mesic habitats and a number form luxuriant bryophyte polsters or mats. Other species of *Encalypta* are very seldom found intermixed in populations of *E. affinis*, and it is the only species that characteristically occurs in late snow-melt habitats.

Encalypta affinis occurs on both acidic and calcareous substrata in western North America. Values from 5.9 to 7.3 (n=29 from 11 different localities) with the mean just subneutral at 6.7 (s.d.=±0.5) have been recorded (Fig. 300). The Ca^{++} concentrations similarly reflect this tolerance of somewhat acidic conditions (Fig. 301, Table 9). However, the range in Mg^{++} concentration is greater than for any other species of Encalyptaceae and a significant proportion of the populations occurred on substrates with higher concentrations of Mg^{++} than did any other species (Fig. 302, Table 9). The tolerance of both acidic and calcareous substrates is reflected in the associates that have been collected with *E. affinis*, some of which are more characteristic of siliceous conditions including *Bartramia ithyphylla*, *Lophozia barbata*, *L. lycopodioides* and *Timmia austriaca*, and others that are generally considered to occur primarily on calcareous substrates including *Blepharostoma trichophyllum*, *Distichium capillaceum*, *Ditrichum flexicaule*, *Myurella julacea*, *M. tenerrima*, *Peltigera horizontalis*, *Pohlia cruda* and the *Solorina* spp. Further studies are needed to investigate the correlation between the occurrence of *E. affinis* and substrates with high Mg^{++} content.

Distribution: The subspecies of *E. affinis* more-or-less complement one another in their patterns of distribution. *Encalypta affinis* subsp. *affinis* predominates in Eurasia where it occurs in montane habitats from the Pyrénées in France, through the Alps in Switzerland-Austria-northern Italy, the Caucasus Mountains and in the Lake Baykal region in Asia. Populations extend as far northward as the montane regions of Scandinavia and towards the arctic coast along the Lena River in northern Asia. In Eurasia, *E. affinis* subsp. *macounii* appears to be restricted to a few localities in Scandinavia. In contrast, *E. affinis* subsp. *macounii* occurs almost throughout the range of the species in western North America from southern Alaska, across central and eastern Yukon Territory to extreme west-central Northwest Territories, then southward from these northerly localities through the Rocky Mountains in British Columbia and Alberta to northern Montana. There are also sporadic records through the Coast Ranges in British Columbia to northern Washington (Fig. 155). In North America, *E. affinis* subsp. *affinis* is restricted to the Brooks Range in northern Alaska, scattered montane localities throughout the Yukon Territory, the Selwyn Mountains, the Mackenzie Delta and the eastern shore of Great Bear Lake in the western Northwest Territories, and the Rockies in north-central British Columbia. From these localities in western North America, *E. affinis* subsp. *affinis* presently appears to be disjunct to the west-central and east-central coasts of Greenland (Fig. 156).

Both *E. affinis* subsp. *macounii* and *E. affinis* subsp. *affinis* are restricted to montane and low arctic habitats in North America. *Encalypta affinis* subsp. *macounii* is more widespread in North America, but within their respective ranges both subspecies are not uncommon. In particular areas of the mountains in western North America, for example, in the Jasper-Banff region of western Alberta, *E. affinis* subsp. *macounii* appears to be of frequent occurrence. Populations of both subspecies characteristically form luxuriant and rather extensive tufts that are generally covered with sporophytes.

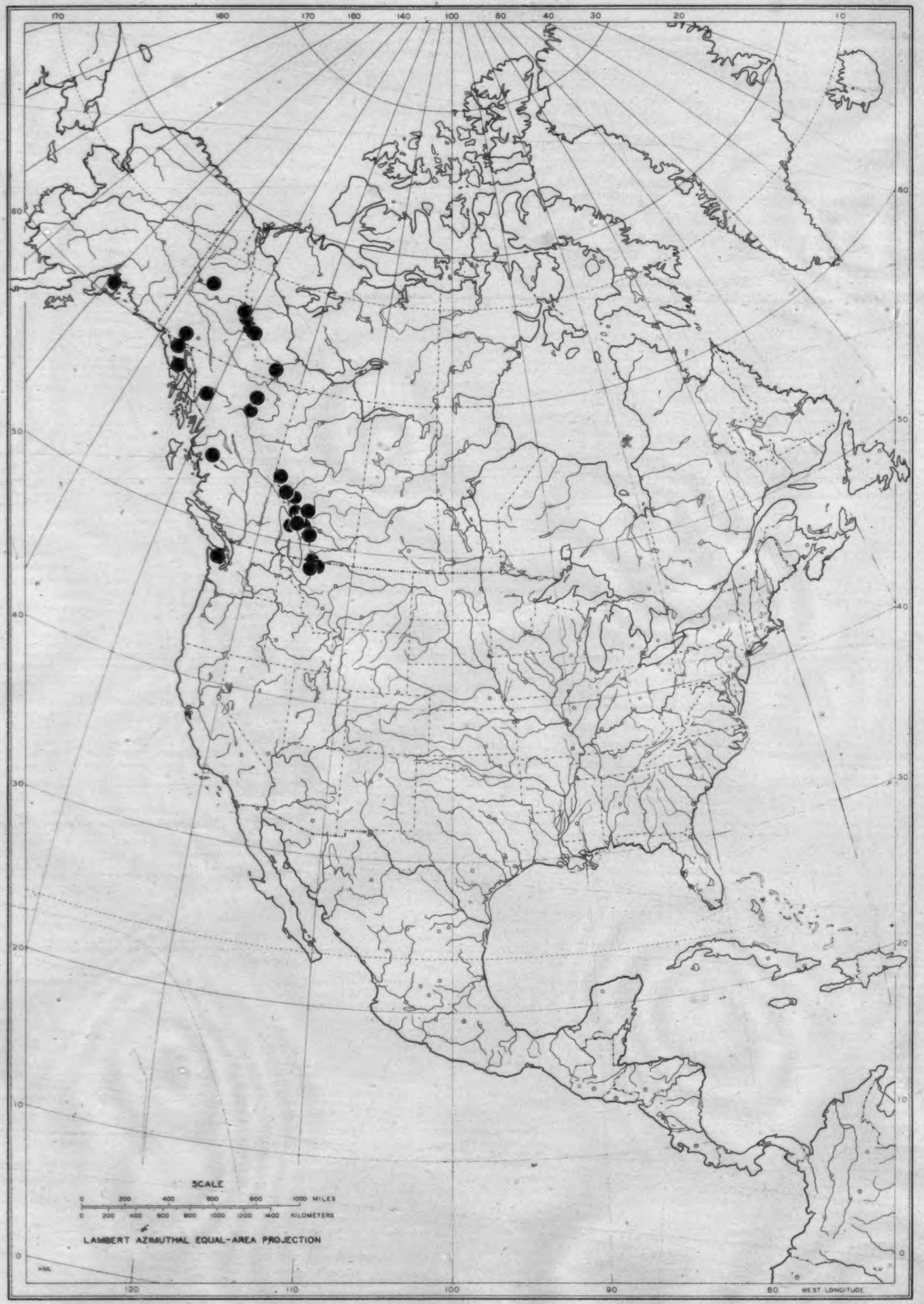
The predominance of *E. affinis* subsp. *affinis* in Eurasia and of *E. affinis* subsp. *macounii* in North America may be related to the effect of the Pleistocene glaciations. In western North America, *E. affinis* subsp. *affinis* is more-or-less restricted to the unglaciated areas of Beringia, while *E. affinis* subsp. *macounii* is more widespread farther south in the mountains of British Columbia and Alberta both in areas that were extensively glaciated and in areas considered to have been ice-free, at least for extended periods of time during the Pleistocene (Packer & Vitt 1974, Horton 1981a).

Phylogenetic Relationships: *Encalypta affinis* is somewhat isolated from all other species of *Encalypta* by the unique feature of papillose basal cells. However, other characteristics suggest a close relationship with *E. brevicolla* and a more distant one with *E. procera*. As noted above, the calyptra of *E. affinis* is virtually indistinguishable from that of *E. brevicolla*, not only in shape and size, but also in color and the occurrence of rather dense papillae over the surface. In some populations of *E. brevicolla*, the capsules have a more-or-less distinctly defined neck. Both *E. affinis* and *E. brevicolla* are characterized

Figure 155. Distribution of Encalypta affinis subsp. macounii in North America.

NORTH AMERICA

No. 2



LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

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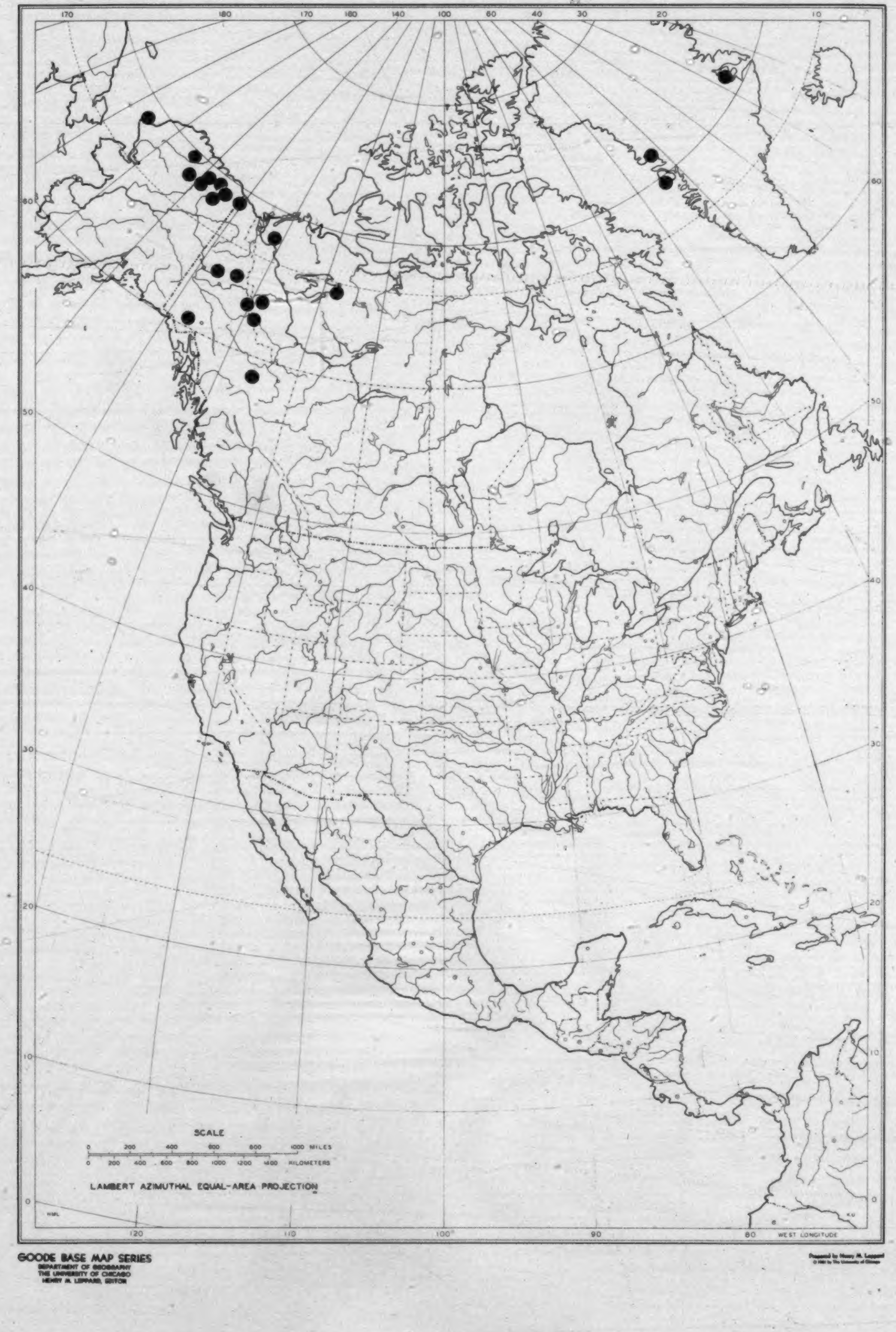
Figure 156. Distribution of *Encalypta* *affinis* subsp. *affinis* in North America.

NORTH AMERICA

No. 2


SCALE
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
120
110
100°
90
80
60
50
40
30
20
10
0
170
180
140
HML

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by a fused, double peristome of lanceolate-linear teeth, with the endostome more-or-less joined basally by a very low membrane. The seta of E. affinis is variable in length, but is relatively long in some populations, as is that of E. brevicolla. Encalypta brevicolla has the seta dark-red throughout, while that of E. affinis is dark-red except near the capsule where it is paler. Plants of E. affinis are invariably characterized by brown tones, while those of E. brevicolla are generally distinguished by black tones, but there are occasional populations of E. brevicolla that feature brown rather than black overtones. The abaxial surface of the costa is densely papillose in the area of the basal and transitional cells in both E. affinis and E. brevicolla. Spores of E. affinis and E. brevicolla are paraisopolar and gemmate.

The calyptra is papillose in E. procera, as it is in E. affinis, and the operculum is conic-rostrate in both. The slender capsules of E. affinis with a narrow rim are reminiscent of those of E. procera. Not only is the peristome of E. procera double, like that of E. affinis, but the teeth and segments are fused for two-thirds of their length. This is in contrast to the condition in E. streptocarpa where the teeth and segments are more-or-less unfused. The seta is dark-red in E. procera, and the calyptra, seta and leaves are characteristically long, as are those of E. affinis. In both E. procera and E. affinis the abaxial surface of the costa is strongly papillose. The spores of E. procera are relatively small, like those of E. affinis.

Specimens Examined: Encalypta affinis subsp. affinis: ALA (5), ALTA (50), BM (1), CANM (10), FI (1), Priv. Herb. D. G. Horton (25), IRK (1), NY (20), O (30), S (40), UBC (7). Encalypta affinis subsp. macounii: ALA (1), ALTA (120), BM (2), CANM (50), H (5), Priv. Herb. D. G. Horton (25), NY (20), O (2), S (4), UBC (25).

ENCALYPTA BREVICOLLA (Bruch, Schimper *et* Gümbel) Bruch *ex* Aongstroem,

Nova Acta Regiae Soc. Sci. Upsal. 12: 362. 1844.

Figs. 10–11, 28, 37, 49, 59–60, 157–175.

Basionym: *Encalypta longicolla* Bruch var. *brevicolla* Bruch, Schimper *et* Gümbel, Bryol. Eur. 3: 28, pl. 5, figs. β1–4, β13, β19. 1838 (Fasc. 4 Mon. 12.5). Type: "dehinc nusquam reperta, nisi in alpibus prope Kongsvold Norwegiae, ubi amicus Kurr varietatum *B.* detexit." (Holotype: "Encalypta brevicolla aus Norwagen unter E. rhabdocarpa gewachsen Kurr. 1828." BM-Schimp.!).

Encalypta subbrevicolla Kindb., Eur. N. Am. Bryin. 2: 295. 1897. Type: "*Amer.* r. Can. northern Labrador: Macoun 1896." (Holotype: "Encalypta subbrevicolla Kindb. n. sp. Amer. N. Labrador J. Macoun 3/8 96" S-Kindb.!; Isotype: NY!).

Encalypta labradorica Kindb., Eur. N. Am. Bryin. 2: 295. 1897. Type: "*Amer.* r. Can. northern Labrador: Macoun 1896." (Lectotype: "Encalypta labradorica Kindb. n. sp. N. Labrador Macoun 30/8 96" S-Kindb.!; Isotypes: NY!, S-Möll.!).

Leersia brevicolla (B.S.G.) Lindb., Musc. Scand. 20. 1879. *Nom. Inval.*

Nomenclatural Notes: (1) A number of early collections of *E. brevicolla* in Sommerfelt's herbarium bear the manuscript name *E. leucostoma*. These beautiful specimens were collected as early as 1816 and 1817, and one of these marked "an nova species" has careful notations of features that distinguish these plants, quite correctly from *E. ciliata* and *E. affinis*, the two species that I consider *E. brevicolla* most likely to be confused with. Apparently Sommerfelt never did publish his name because Bruch's *E. brevicolla* is written above *leucostoma*, presumably at a later date.

(2) The specimen of *E. subbrevicolla* in Kindberg's herbarium is designated the holotype because it is the only one of this taxon in S. The specimen in NY was probably sent to E. G. Britton by Macoun and in all likelihood Kindberg never saw it. In contrast, there are two specimens of *E. labradorica* in S, so a lectotype has been selected.

Diagnosis and Differentiation: Perhaps the most distinctive feature of *E. brevicolla* is the short, white and densely papillose peristome. Although there are two layers these are fused giving the appearance of a single row of teeth. This species is also characterized by a papillose, opaque and slightly puckered calyptra with a long, rather distinctly defined rostrum and long cylinder. The cylinder is slightly tapered basipetally and then ultimately is slightly, but distinctly, constricted just above a short, pendent fringe, which is generally rather ragged-looking because the segments are irregular and many are more-or-less broken off. The perfectly smooth and turgid-looking capsules are narrowly cylindric to cylindric with a slightly expanded mouth. Coloration of the upper part of the capsule is a distinctive, irridescent crimson-red. The seta is dark-red throughout. In most populations, the apices of the green leaves are blackened and some of the lower leaves are not infrequently blackened throughout, which gives an overall scorched appearance to the relatively large plants. Microscopic features of the leaves of *E. brevicolla* include the distinctly differentiated basal laminal cells with dark-orange transverse and yellow longitudinal walls that contrast with the broad, marginal border of greenish cells. The abaxial surface of the transitional cells is densely papillose with enlarged papillae that extend to the basal cells. In the area of the transitional cells the costa is similarly papillose, but it is more-or-less smooth distally. There are one to two rows of stereids in a transverse section of the costa. The brown spores are paraisopolar and the surface is more-or-less covered by rather large, but somewhat flattened, gemmae.

Encalypta brevicolla might most readily be confused with *E. ciliata*, with which it quite frequently occurs in mixed collections, or with *E. affinis*. *Encalypta ciliata* is differentiated by a smooth, transluscent calyptra with a more distinctly defined rostrum and a shorter cylinder. At the base of the cylinder there is a distinct, narrow horizontal extension from which a precisely segmented fringe is pendent or flaring. Capsules of *E. ciliata* are similarly short and broad as they are in *E. brevicolla*, but there is a distinct constriction below the mouth of the capsule and coloration is typically yellow or orange. The peristome of *E. ciliata* is quite different from that of *E. brevicolla*, both in the dark-orange coloration and the grimmioid shape of the teeth. Also, the peristome consists of a single layer of teeth. The seta is yellow to orange with just a tinge of bright-red at the base of the capsule. Leaves are mucronate with the margins always narrowly recurved basipetally from the mid-portion and the prominent, shiny and smooth costa is distinctively yellow to golden-brown in color. The yellow tones that characterize

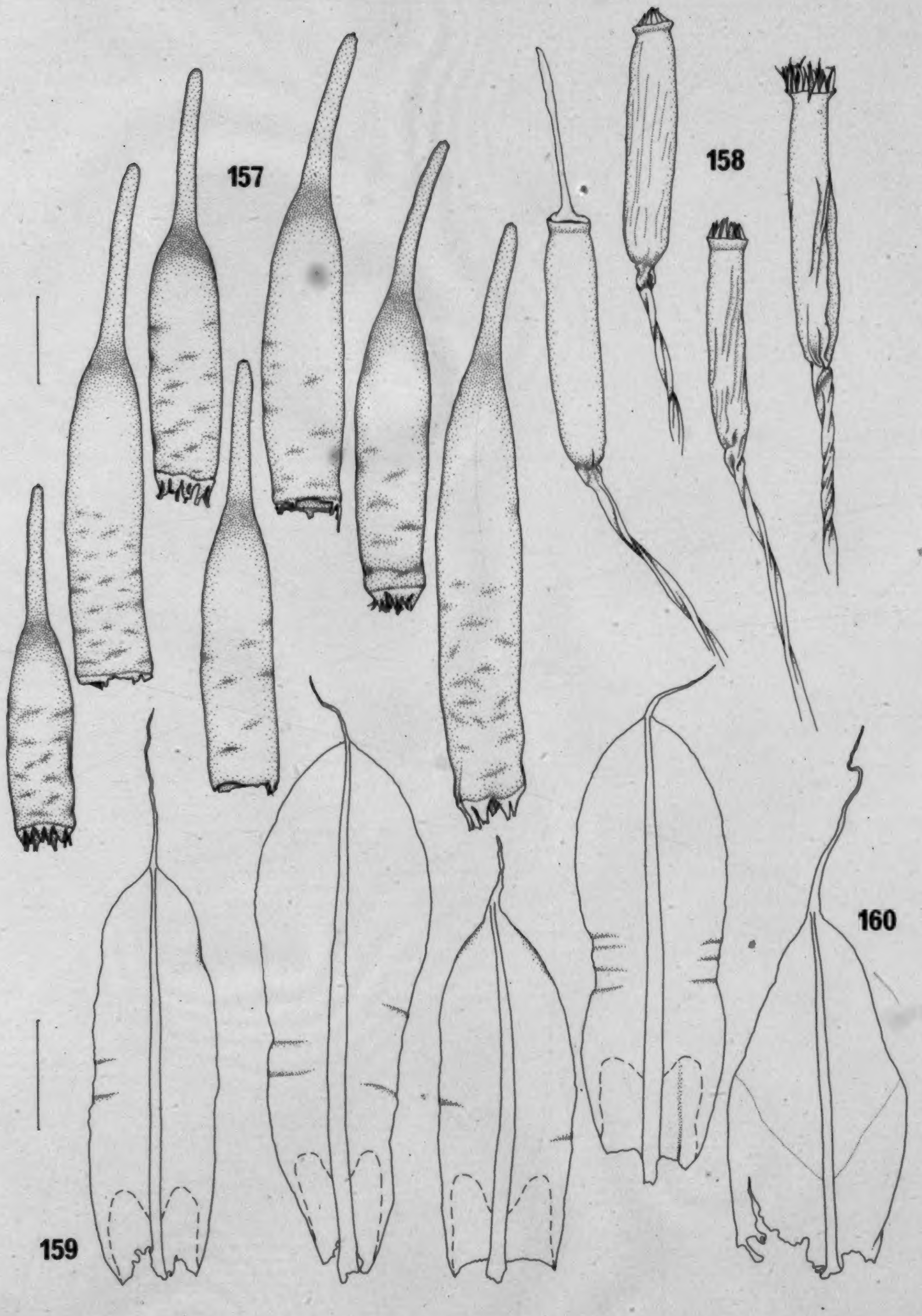
Figures 157-160. **Encalypta brevicolla.** Scale=1 mm.

Fig. 157. Calyptrae.

Fig. 158. Capsules.

Fig. 159. Vegetative leaves.

Fig. 160. Perichaetial leaves.



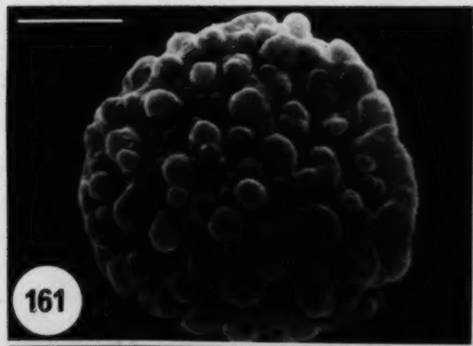
Figures 161-166. ***Encalypta brevicolla.*** **Distal Surface of Spores.**

Fig. 161. Scale=10 μm.

Fig. 162. Scale=4 μm.

Figs. 163-165. Scale=10 μm.

Fig. 166. Scale=4 μm.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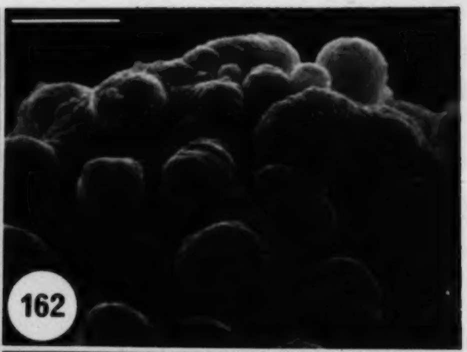
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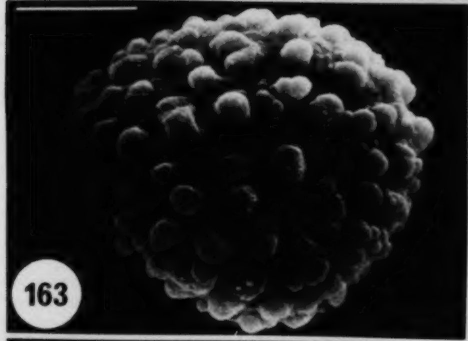
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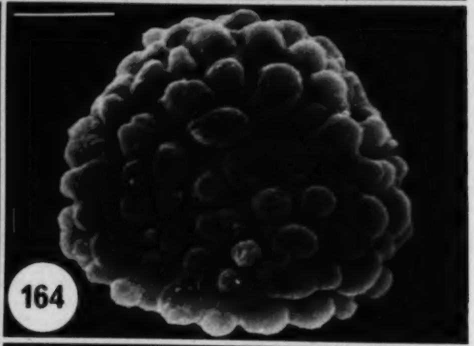
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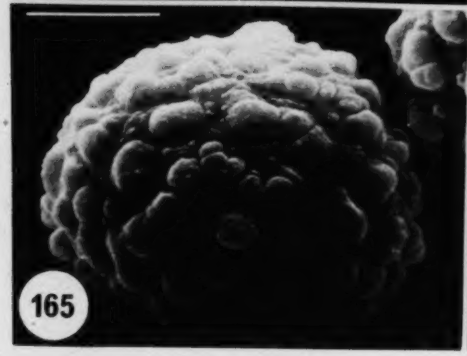
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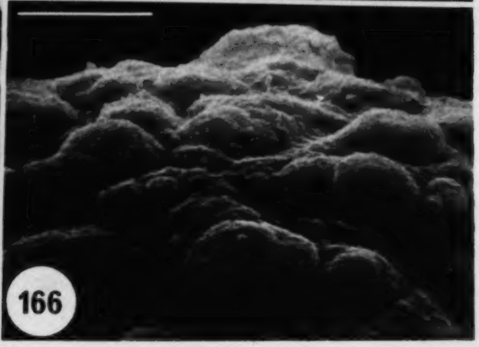
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Figures 167-172. Encaypta brevicolla.

Figs. 167-171. Proximal Surface of Spores.

Fig. 167. Scale=10 μm.

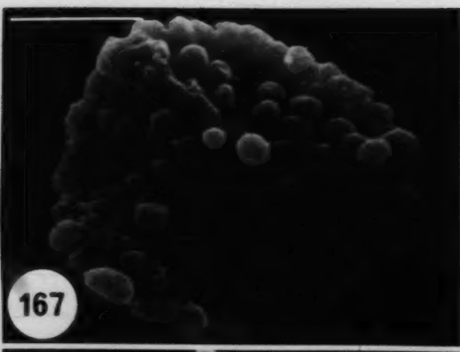
Fig. 168. Scale=4 μm.

Fig. 169. Scale=10 μm.

Fig. 170. Scale=4 μm.

Fig. 171. Scale=10 μm.

Fig. 172. Peristome with smooth teeth from Oregon population. Scale=100 μm.



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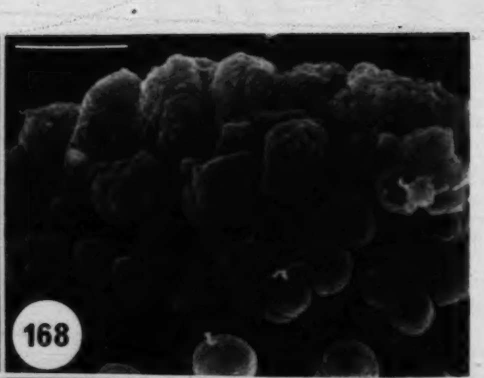

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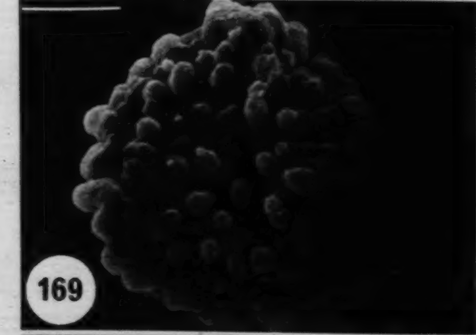

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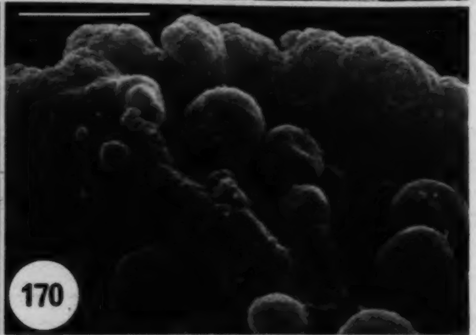

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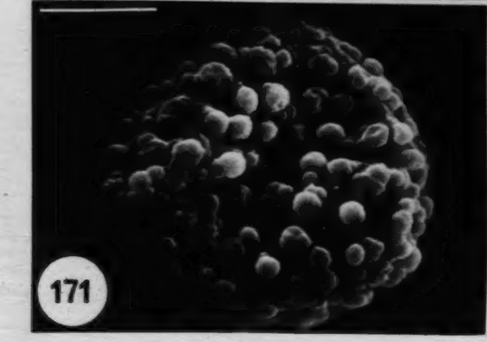

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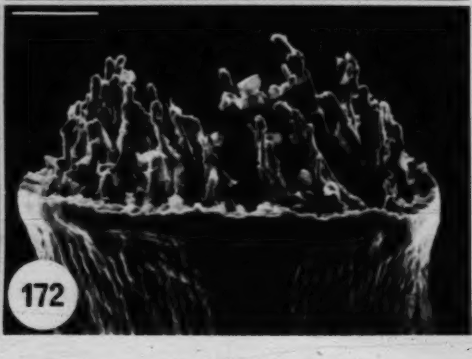


172

plants of *E. ciliata* contrast with the true-green and black coloration in the vegetative plants and the deep-red coloration of the sporophyte of *E. brevicolla*. On the basis of microscopic features of the leaves, *E. brevicolla* and *E. ciliata* are virtually indistinguishable, except that the abaxial surface of the costa is smooth or only slightly papillose in *E. ciliata* and the coloration of the basal cells is not as dark because the longitudinal walls are hyaline. The spores of *E. ciliata* can be differentiated by the very distinct triradiate mark and numerous radial plicae characteristic of the proximal surface. While the ornamentation of the distal surface is variable, the gemmae characteristic of *E. brevicolla* do not occur.

The calyptra of *E. affinis* is virtually identical to that of *E. brevicolla* in all respects, except that in *E. affinis* the cylinder is slightly longer and the rostrum is not quite so distinctly defined. *Encalypta affinis* can be differentiated by the narrower and longer, delicately striate, capsules that are pale-golden with a very narrow, red rim. Also, the peristome teeth are consistently pink in coloration (only very rare populations of *E. brevicolla* have teeth that are a very pale peach color), but are otherwise rather similar in shape, except that those of *E. affinis* are longer than those of *E. brevicolla*. The coloration of the seta of *E. affinis* is very similar, except that it is characteristically orange or yellowish in the upper part. Coloration of the vegetative plants is a fairly reliable differentiating feature. The leaves of *E. affinis* are dark-green with the apices and lower leaves dark-brown; very seldom are there the blackish overtones that are characteristic of *E. brevicolla*. The characteristic most reliable for distinguishing *E. affinis* from *E. brevicolla* is the strongly papillose walls of the basal laminal and, particularly, the basal marginal cells. Other useful microscopic features include the lack of differentiation of a basal marginal leaf border and the transverse section of the costa with five to six rows of stereids. The gemmae that characterize spores of *E. affinis* are smaller than those of *E. brevicolla*.

Vegetative plants of *E. rhaptocarpa* and of *E. brevipes* are quite similar to and often grow intermixed with those of *E. brevicolla*. However, the rostrum of the calyptra of *E. rhaptocarpa* is generally shorter than that of *E. brevicolla* and there is no constriction at the base of the cylinder, which is either entire or erose, but not fringed. (The calyptra of *E. vittiana* is fringed, but this taxon can be separated by the same features as *E. rhaptocarpa*, as follows.) The capsule of *E. rhaptocarpa* is differentiated by the prominent, longitudinal, red ribs, and the single peristome consists of teeth that are lanceolate and dark-orange. Forms of *E. rhaptocarpa* with a more-or-less white peristome and capsules that lack prominent red ribs are particularly difficult to distinguish from *E. brevicolla*. However, the shape of the peristome with only one vertical row of cell plates on the outer surface of each tooth and the longitudinally plicate capsules are features that should differentiate these taxa. The most obvious features that differentiate *E. brevipes* from *E. brevicolla* are the exceptionally short rostrum of the calyptra, the lack of a peristome and the very short seta. In mixed collections, the setae of *E. brevipes* are always shorter than those of *E. brevicolla*.

Description: *Plants* to 25 mm tall, light-green to dark-green and blackened above in most populations, fewer green to olive-green and dark-brown, brown below; ± branched. *Stem* in transverse section with central strand absent. *Brood bodies* absent. *Axillary hairs* sparse. *Leaves* when dry irregularly ± twisted and incurved above, laminae ± undulate and inflexed to conduplicate; 2.0-6.0 mm long, 1.0-1.8 mm wide, oblong, some with slight constriction in the mid-portion, to obovate, apex blackened in many populations, dark-brown in very few, ± abruptly narrowed to hyaline hair-point that is 2 mm long and ± cucullate; *margins* plane in virtually all populations, in 1 or 2 populations 1 margin very narrowly and shortly recurved in the mid-portion of very few leaves. *Costa* excurrent, abaxial surface inconspicuously keeled above, somewhat shiny in the upper part and dull below, green to brownish in older leaves, smooth basally, then strongly and densely papillose in region of transitional cells, less strongly so distally; in transverse section with 2-3 rows ventral cells, begleiters undifferentiated, 1-2 rows of stereids. *Upper laminal cells* 12-18μm wide, 12-20(25)μm long, with 2-4 papillae per cell, each ± distinctly "c"-shaped; *upper marginal cells* 12-16μm wide, (8)12-14μm long; *transitional cells* densely papillose to basal cells on abaxial surface, papillae large and much-branched with long branches, some "o"-shaped, on adaxial surface smooth well above basal cells; *basal laminal cells* m long, 14-23μm wide, prominent, transverse walls dark-orange, strongly thickened particularly at corners and smooth, longitudinal walls yellow, thin and smooth, superficial walls smooth, entire to irregularly ± perforated; *basal marginal cells* distinctly differentiated in 8-12 rows. Goniautoicous. Perichaetial leaves oblong above ± sheath-like base, abruptly to quickly narrowed to hair-point; perigonial leaves 0.8-1.5 mm long, broad and sheath-like below, apex acuminate and mucronate to cuspidate; perigonial paraphyses with walls smooth, or with sparse low papillae on upper 1 or 2 cells.

Seta 2.5-17.0 mm long, flexuose to erect, slightly twisted sinistrorsely below, ± strongly twisted dextrorsely just below capsule, shiny and dark-red in most populations to orange, dull-orange when older; in transverse section 135-210 μm in diameter. Capsule 1.1-3.5 mm long, when dry narrowly-cylindric to cylindric below ± expanded mouth, some with slight constriction just below mouth, mouth slightly oblique in many populations, capsules ± tapered basipetally and quickly to abruptly contracted to seta through short neck, some with strong constriction just above neck, smooth and ± turgid, golden-brown below and irridescent crimson-red in the upper part with color progressively darker to crimson-red rim, young capsules delicately and slightly obliquely striate, greenish with red rim, when old ± collapsed, some ± spirally striate and twisted, some with short, longitudinal splits from mouth, rust-colored; exothecial cells 45-160 μm long, 16-27 μm wide, in longitudinal rows, in transverse section walls evenly thickened on external surface, 4.5-5.0 m thick; rim cells in 4-6 ± regular, longitudinal rows, 12-28 μm wide, 6-23 μm long, walls slightly thickened; stomata superficial, 4-8, scattered or ± restricted to capsule base, 39-41 μm long, 23-32 μm wide. Peristome 0.2-0.3 mm long, in 2 concentric layers, exostome teeth and endostome segments fused, 16, ± erect to inflexed or slightly reflexed, linear-lanceolate, some ± longitudinally split, white, pale peach-colored in very few populations, exostome outer surface with 2 vertical rows of cell plates, densely irregularly papillose, smooth in 1 population, inner surface with trabeculae fused to endostome, endostome ± joined basally by very low membrane that extends to or only slightly above capsule rim, inner surface with 2 vertical rows of cells plates basally, densely irregularly papillose, smooth in 1 population. Operculum plane-convex and rostrate, 2.0-2.2 mm long. Annulus undifferentiated. Spores brown, paraisopolar to heteropolar, in polar view radially symmetric and circular to slightly triangular, 30-42 μm, in equatorial view polarly asymmetric and concave-convex, 30-42 μm X 23 μm, proximal surface with indistinct triradiate mark on some, ± densely gemmate to verrucate, gemmae or verrucae 2.8–3.2 μm in diameter, surface ± irregular and minutely granular between protuberances; distal surface ± densely gemmate to verrucate, gemmae 3.5–6.0 μm in diameter, proximal gemmae appear more detached than those on distal surface. Calyptra (3.2)4.2–8.0 mm, extends well below capsule, long-cylindric and distinctly contracted, indistinctly in 1 population, to slightly curved or erect, long rostrum that is (1.2)1.6–2.2 mm long, cylinder tapered slightly basipetally in many populations, and slightly, distinctly constricted at base, some with slight horizontal or oblique expansion, fringed, segments ± regularly narrow-trapezoidal, 0.3 mm long, pendent to incurved to slightly flared, ± broken off, calyptra golden-brown to dark-brown distally with a brownish to whitish fringe, dull to somewhat shiny, opaque in most populations, transluscent in few, ± strongly papillose, papillae longest and sharpest on rostrum and neck, lower and rounded on cylinder; in transverse section cylinder with 2–3(4) layers of cells with small lumina and very thick walls; fringe with 1 row of cells, walls exceptionally thickened in 2 layers, outermost yellowish, inner hyaline; in superficial view fringe cells short- to long-oblong with 2–3 rows of quadrate cells at juncture with cylinder. Chromosome number unreported.

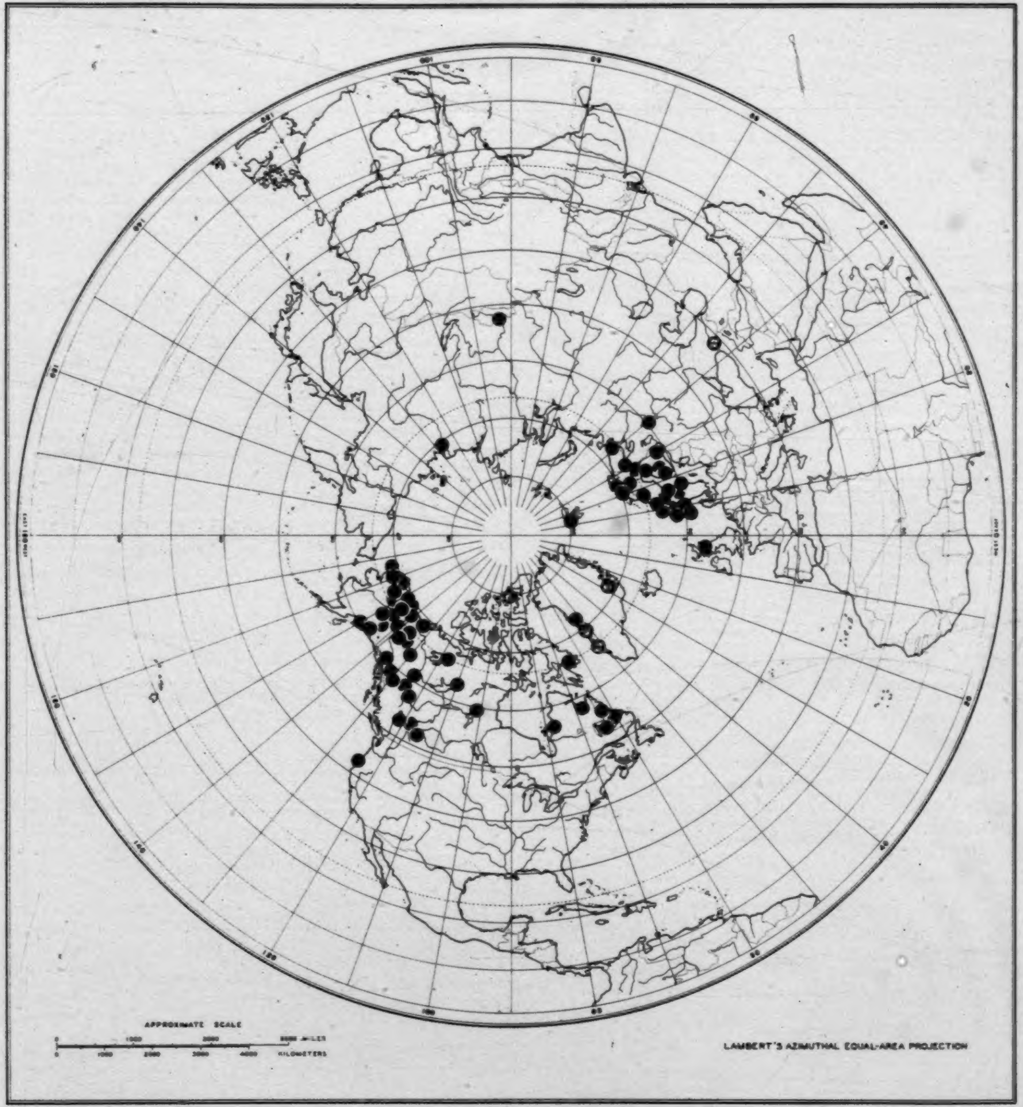
Habitat: Populations of E. brevicolla occur in montane and tundra habitats in relatively exposed, windswept and therefore probably quite xeric sites. However, the microhabitat is generally protected, in some instances by surrounding vascular plant vegetation and in others by small solifluction overhangs; therefore, it is probably somewhat more mesic than the surrounding macrohabitat. Also, E. brevicolla very seldom occurs on the top of exposed knolls where the snow is swept free by wind in winter. In contrast, E. rhaptocarpa, with which E. brevicolla quite commonly is intermixed, does grow in such habitats and is apparently tolerant of greater exposure and more xeric conditions than E. brevicolla. Encalypta brevicolla also occurs on rock outcrops, in crevices and on ledges, wedged among stones or roots of vascular plants. In this habitat, it occurs at elevations well below treeline.

Undoubtedly, one of the most important factors governing the occurrence of E. brevicolla at different sites within its range is the nature of the substrate. Both Mårtensson (1956) and Nyholm (1954) reported E. brevicolla to occur in calcareous habitats. Likewise, Crum (1960-61) noted that it is characteristic of calcareous substrates in North America. In contrast, Brotherus (1924) reported *E. brevicolla* to occur in association with "...kalkarmer Felsarten.". Analyses of soil samples collected in western North America indicate a relatively narrow range of tolerance. The pH varied from 5.0-6.0 (n=37 from 20 different localities) with a mean of 5.4 (s.d.=±.48) (Fig. 300), and Ca^{++} and Mg^{++} concentrations are correspondingly low (Figs. 301-302, Table 9). The exclusive assocation of *E. brevicolla* with rather acidic substrates is reflected in many of the species that are sporadically associated with it, as these are also generally considered to be indicative of subneutral to distinctly acidic conditions. These include *Amphidium lapponicum* (Hedw.) Schimp., *Anastrophyllum minutum* (Schreb.) Schust., *Bartramia ithyphylla* Brid., *Cnestrum schisti* (Wahlenb.) Hag., *Cynodontium tenellum* (B.S.G.) Limpr., *Dicranum brevifolium* (Lindb.) Lindb., *Encalypta brevipes, E. ciliata, E. rhaptocarpa, Hedwigia ciliata* (Hedw.) P.-Beauv., *Paraleucobryum enerve* (Thed. *ex* C. J. Hartm.) Loeske, *Pogonatum alpinum* (Hedw.) Roehl, *Polytrichum piliferum* Hedw., *Rhacomitrium canescens* (Hedw.) Brid., *R. heterostichum* (Hedw.) Brid., *R. lanuginosum* (Hedw.) Brid., *Saelania glaucescens (Hedw.) Bomanss. et* Broth., and *Tritomaria quinquedentata* (Huds.) Buch. The fact that many of these same associates occur with *E. brevicolla* in northern Europe leads me to believe that the occurrence of this species is similarly limited by substrate-type there.

Distribution: *Encalypta brevicolla* has a circumpolar distribution in alpine, subarctic and arctic regions, with a few localities disjunct farther south (Fig. 173). In North America, the records of *E. brevicolla* are concentrated along the western Cordillera. It is reported from Alaska in the Brooks Range, the Fairbanks area, and the Alaska Range, and the Chugach and Kenai Mountains; from the Yukon Territory in the British Mountains, the Ogilvie, southern Richardson and Wernecke Mountains, and along the eastern border in the Selwyn Mountains; from the western Northwest Territories in the Mackenzie Mountains; from northern British Columbia in the Coast Mountains and the Rocky Mountains, and the Columbia Mountains farther south ; and from Alberta in the Rocky Mountains. The locality in the Coast Range of southern Oregon is disjunct. East of the Rockies, *E. brevicolla* is reported from a number of widespread localities including the

Figure 173. Distribution of *Encalypta brevicolla*.

WORLD, NORTHERN HEMISPHERE **No. 201PN**


APPROXIMATE SCALE
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LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION

GOODE'S SERIES OF BASE MAPS
HENRY M. LEPPARD, EDITOR

Prepared by Henry M. Leppard
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Mackenzie Delta and the eastern shore of Great Bear Lake in the western Northwest Territories; northwestern Manitoba; the eastern shore of Hudson Bay and the Fort Chimo area of Ungava Bay in northern Quebec; and several localities in Labrador (Fig. 174). In the Canadi Archipelago, E. brevicolla is known from the Pangnirtung area of Baffin Island, the Truelove Lowland on Devon Island and western Axel Heiberg Island (Kuc (1973a) – indicated on Fig. 174 by an open circle because specimens that were requested have not been made available to me). In Greenland, it is known from localities along the east and west coasts in the central and southern parts of the Island (Crum (1960–61) – indicated on Fig. 174 by open circles because specimens requested from C have not been made available to me).

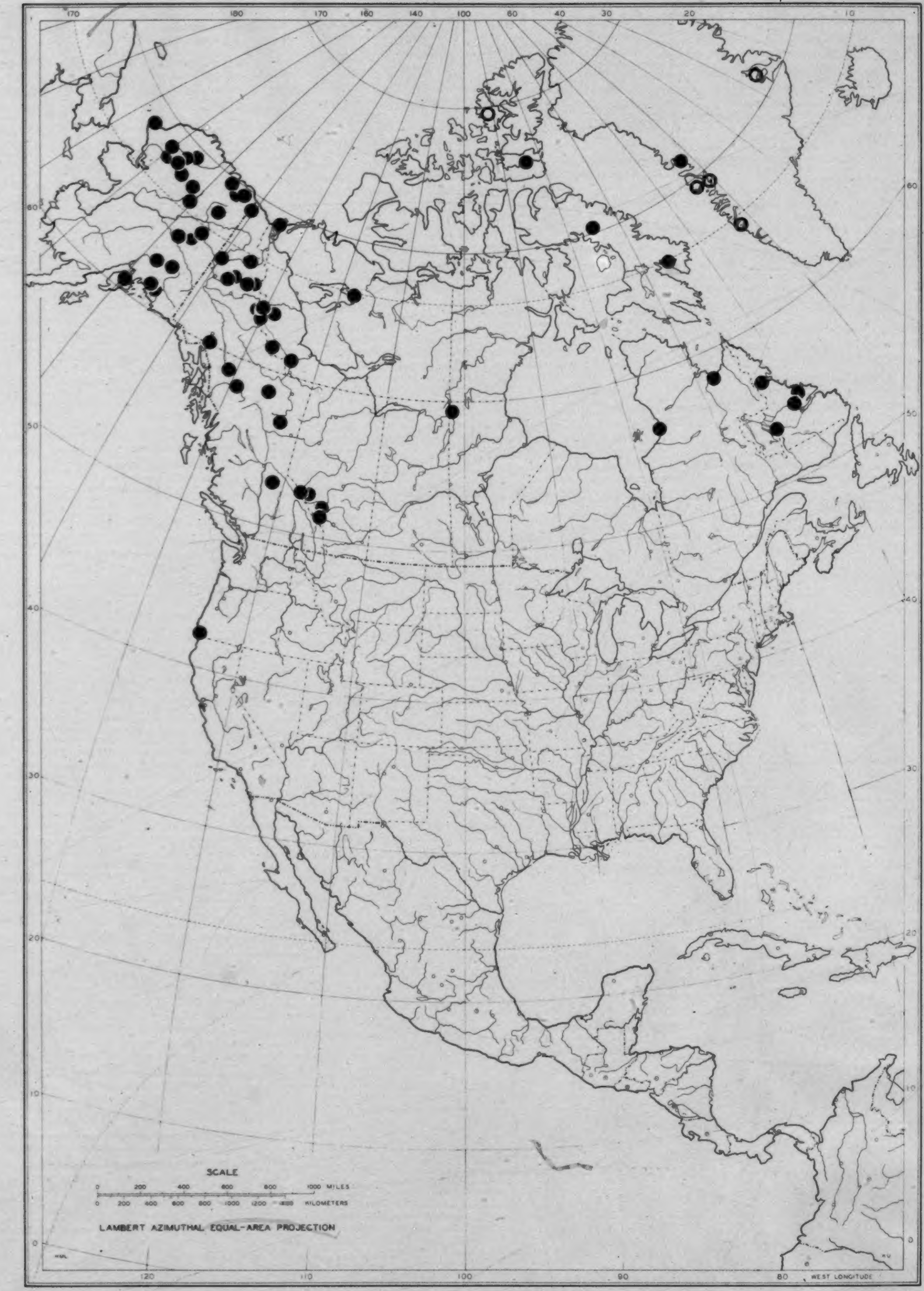
In Eurasia, populations of E. brevicolla appear to be concentrated in Scandinavia. The species is reported from Norway from a single locality in Troms and one in Finmark, as well as numerous continental and a few scattered coastal localities in the south and central parts of the country as far north as Snasa; from Sweden from Lule Lappmark, Jämtland and the Uppsala area; from Finland from most interior provinces including Lapponia enontekiensis, Lapponia inarensis, Lapponia kemensis, Ostrobottnia borealis, Kuusamo, Ostrobottnia kajanensis, Tavastia borealis, Savonia borealis, Karelia borealis, Tavastia australis, Savonia australis, as well as coastal stations in Satakunta and Regio aboënsis; from Karelian A.S.S.R. from the former Finnish provinces of Karelia ladogensis and Lapponia ponojensis (Brotherus 1924) (Fig. 175). Encalypta brevicolla has been recently recorded from Svalbard (Frisvoll 1978) (Fig. 173) and from the British Isles in Scotland (Horton 1980) (Fig. 175). However, this latter locality is based upon a single specimen collected in 1871 and, to my knowledge, no other specimens from Great Britain exist. Encalypta brevicolla is reported from a disjunct locality in the Ural Mountains and from near the mouth of the Lena River (Fig. 173).

Variation: The disjunct Oregon population of E. brevicolla (Wagner 1921 ALTA) is quite strikingly differentiated from all other Northern Hemisphere populations in two respects. The peristome teeth are perfectly smooth (Fig. 172) and the rostrum of the calyptra is ill-defined as it is only very gradually narrowed from the cylinder, which is much longer than is characteristic for this species (Fig. 157 – right). I hesitate to give any

Figure 174. Distribution of *Encalypta brevicolla* in North America.

NORTH AMERICA

No. 2



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WEST LONGITUDE

GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

Prepared by Henry M. Leppard
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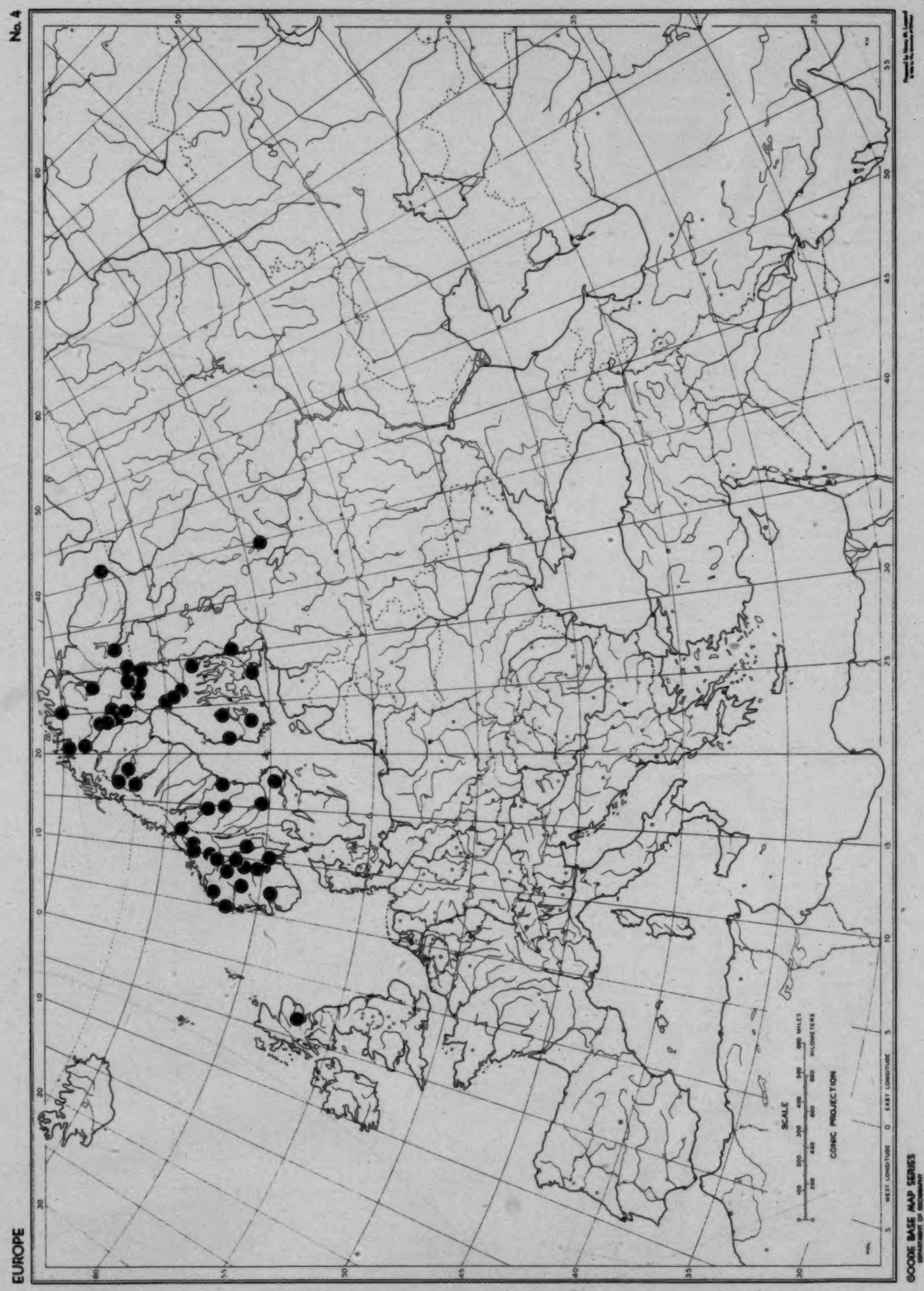
Figure 175. Distribution of Encalypta brevicolla in Europe.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EAST LONGITUDE
GOODE BASE MAP SERIES
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nomenclatural rec these differences at the present time when they have been found to occur in a single population and may merely represent phenotypic responses to some extreme environmental condition. It is noteworthy that a population of *E. brevipes* from northern Oregon that is similarly disjunct is also slightly differentiated from other populations of that species (see discussion of Variation under *E. brevipes*).

Phylogenetic Relationships: *Encalypta brevicolla* appears to be most closely related to *E. affinis* (see discussion of Phylogenetic Relationships of *E. affinis*), *E. brevipes* and *E. ciliata*. It is primarily on the basis of vegetative similarities that a relationship between *E. brevicolla* and *E. brevipes* is suggested. However, *E. brevipes*, like *E. brevicolla*, has an opaque calyptra with the base of the cylinder somewhat constricted and fringed, and the capsule is smooth and turgid. The vegetative plants of *E. brevipes* differ but little from those of *E. brevicolla*. There are the same blackish overtones, the leaves are virtually identical in shape and are similarly hair-pointed with plane margins. Also, there is a well-defined basal marginal border.

In contrast, the features that link *E. ciliata* and *E. brevicolla* are almost all associated with the sporophyte. As in *E. brevicolla*, the calyptrae of *E. ciliata* are long-rostrate and fringed, and the smooth capsules are relatively short and broad. Vegetative features of *E. ciliata* that suggest a relationship with *E. brevicolla* include the well-defined basal laminal cells with orange walls and the broad marginal border of greenish cells.

Specimens Examined: ALA (20), ALTA (80), BM (25), BP (11), CANM (20), E (3), Priv. Herb. J.-P. Frahm (1), G (7), H (75), H-Sol (16), Priv. Herb. D. G. Horton (40), HSC (7), IRK (1), M (12), MICH (9), NFLD (4), NY (18), O (95), PC (12), S (12), TRH (6), UBC (8).

ENCALYPTA BREVIPES Schljakov,

Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Komarova
Akad. Nauk SSSR 7: 227, pl. 1. 1951.
Figs. 52, 176-189.

Type: "Sovral 8 VIII 1948 R. N. Schljakov." (Holotype: LE – loan requested, but not received).

Diagnosis and Differentiation: Encalypta brevipes is characterized by a calyptra with an exceptionally short rostrum. The combination of this feature and leaves with long, hyaline hair-points is so distinctive that plants with emergent calyptrae, but lacking mature sporophytes, can scarcely be mistaken for any other species of Encalypta. Other characteristics of the calyptra include the slightly puckered cylinder with a slight, irregular constriction and/or more-or-less oblique expansion at the base, and a pendent fringe. However, the fringe is more-or-less broken off in many populations once it is exposed. There is never any suggestion of a peristome and the mouth of the capsule is bordered by a broad crimson-red "cuff" of exceptionally thick-walled cells. The seta is so short that the capsule almost appears emergent rather than exserted. Margins of the leaves are plane and the hair-points are relatively stout, particularly at the point of juncture with the leaf apex. The vegetative portions of the plants are generally light- to dark-green with the apices of the leaves and some of the lower leaves more-or-less blackened in many populations. Microscopically, E. brevipes is defined by leaves with the costa more-or-less smooth on the abaxial surface and a relatively small group of basal cells with the transverse walls pale and yellowish and the longitudinal walls hyaline. This lack of dark coloration in the basal cells makes them rather inconspicuous. There is a broad marginal border of greenish cells that extends to the base of the leaves. The papillae on the transitional cells do not reach the basal cells on either surface. Spores are dark-brown and paraisopolar with a verrucose-reticulate surface.

Encalypta brevipes is very similar to E. brevicolla in some structural features and to E. ciliata in others. Furthermore, both the latter species quite commonly occur intermixed in populations of E. brevipes. Encalypta ciliata is differentiated by a

Figures 176-181. **Encalypta brevipes**. Scale=1 mm.

Fig. 176. Habit.

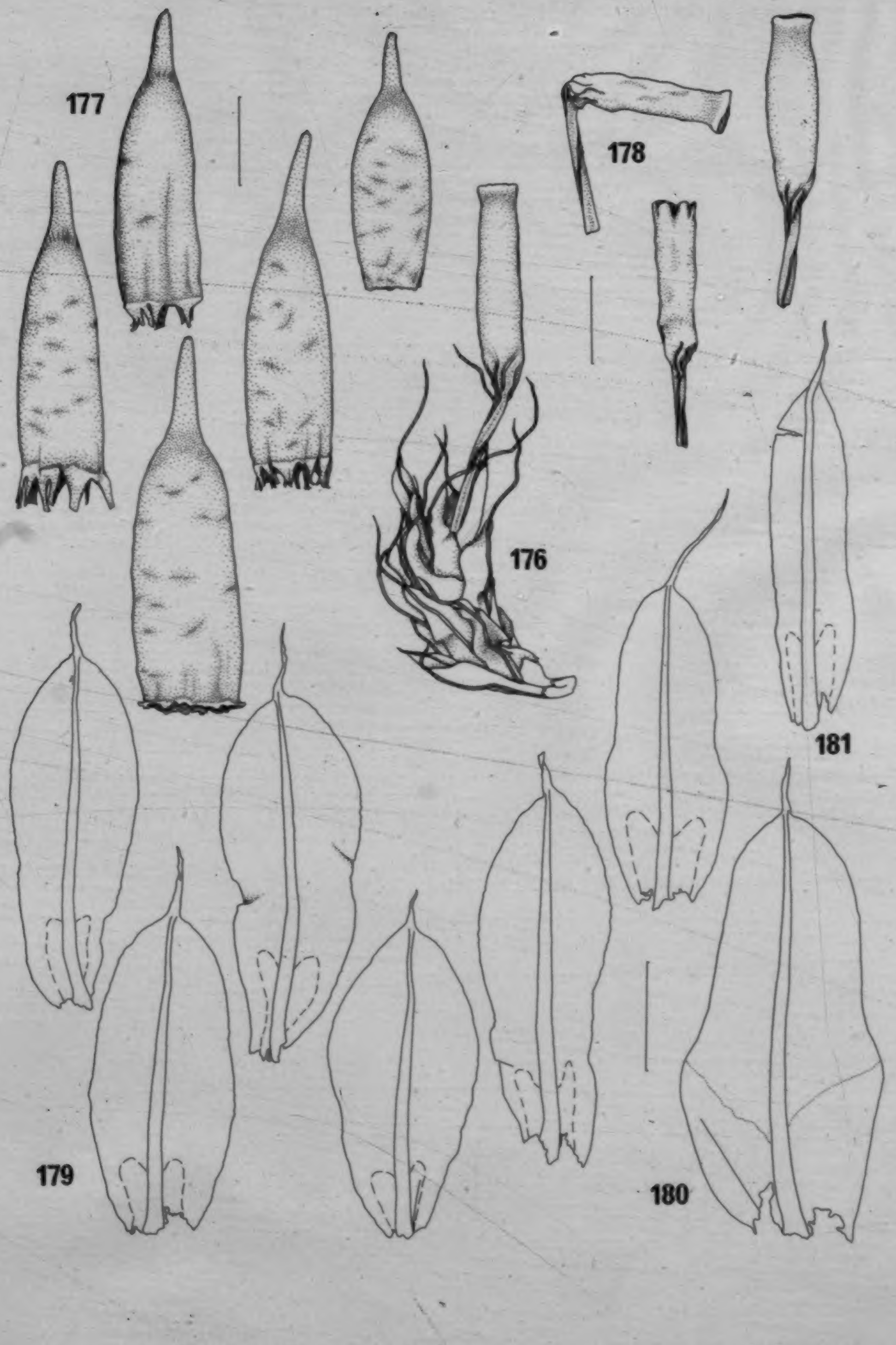
Fig. 177. Calyptrae.

Fig. 178. Capsules.

Fig. 179. Vegetative leaves.

Fig. 180. Vegetative leaf from Oregon population.

Fig. 181. Perichaetial leaves.



Figures 182-187. *Encalypta brevipes* Spores.

Figs. 182-183. Distal surface.

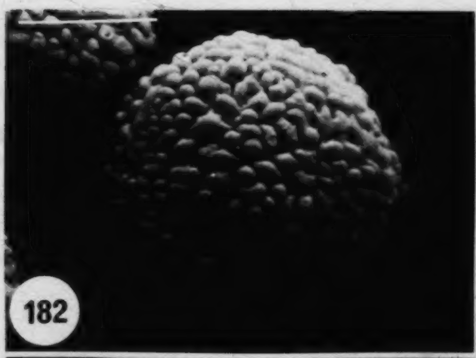
Fig. 182. Scale=20 µm.

Fig. 183. Scale=10 µm.

Fig. 184. Tetrad. Scale=20 µm.

Figs. 185-186. Proximal surface. Scale=20µm.

Fig. 187. Proximal surface. Scale=10µm.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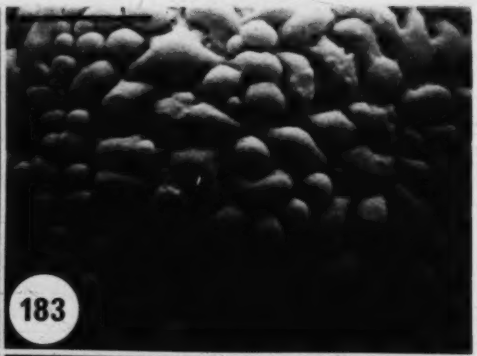
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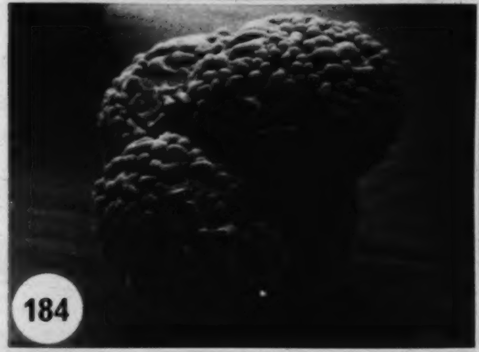
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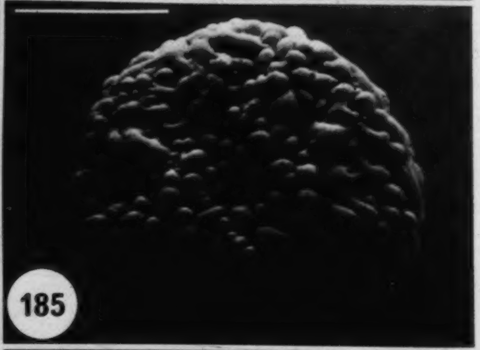
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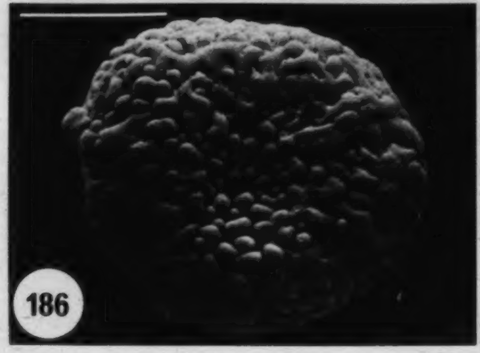
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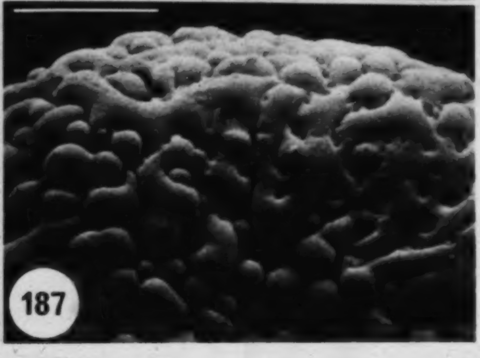

187

long-rostrate calyptra with a distinct, horizontal extension from which the precisely segmented fringe is pendent or flaring. Straw-yellow tones in the capsule and seta are characteristic. However, the shape of the capsule is very similar to that of E. brevipes and this likeness is exemplified when the peristome teeth are broken off, as is quite frequently the situation in populations of E. ciliata. Also, older capsules of E. ciliata are orange and then very similar to those of E. brevipes. Particularly reliable for differentiating E. ciliata are the invariably mucronate leaves with the margins narrowly recurved basipetally from the mid-portion. Microscopically, the basal cells of the leaves in E. ciliata are much more prominent with dark-orange transverse and longitudinal walls, and the marginal border is not quite as wide as that of E. brevipes. Also, the papillae on the abaxial surface of the transitional cells extend to the basal cells. Spores of E. ciliata are best differentiated by the distinct trilete mark on the proximal surface. Sculpture of the distal surface is variable and in some populations a verrucose reticulum that is similar to that which occurs in E. brevipes has been observed.

Most of the features that differentiate E. brevicolla from E. brevipes are sporophytic. In E. brevicolla, the rostrum of the calyptra is longer, as is the calyptra itself. Similarly, the seta is longer. The vegetative plants of E. brevicolla and of E. brevipes are very similar. However, in E. brevicolla the hair-point of the leaves is narrower at the juncture with the leaf apex than it is in E. brevipes, and the costa is papillose in the region of the transitional cells. There are rather subtle differences in the coloration of capsules of E. brevicolla that differentiate them from those of E. brevipes. The crimson-red at the mouth of capsules of E. brevicolla grades basipetally into the golden-brown color of the lower portion of the capsule, whereas in E. brevipes the red "cuff" at the mouth is generally very abruptly defined from the golden color of the rest of the capsule. Microscopically, the basal leaf cells of E. brevicolla are more clearly defined with the transverse walls dark-orange and the longitudinal walls yellow. The basal marginal border is somewhat narrower than that in E. brevipes and the papillae on the abaxial surface of the transitional cells extend down to the basal cells. Spores of E. brevicolla are quite different with the exospore elaborated by relatively large, rounded gemmae or verrucae.

Description: Plants to 13 mm tall, light-green to dark-green and ± blackened above in most populations, some green to olive-green and ± dark-brown above, brown below; ± branched. Stem in transverse section with central strand absent. Brood bodies absent. Axillary hairs sparse. Leaves when dry irregularly ± twisted and incurved, laminae inflexed to conduplicate; 2.0-4.0 mm long, (0.8)1.0-1.5 mm wide, oblong to broadly-oblong, some with slight constriction in mid-portion, or oblong from ± broadly ovate base, elliptic-oblong, to obovate, apex blackened in many populations, dark-brown in very few, abruptly narrowed to stout, hyaline hair-point that is 2 mm long; margins plane. Costa slightly tapered distally in virtually all populations, in 1 population equally strong and prominent throughout, excurrent, abaxial surface inconspicuously keeled above in virtually all populations, conspicuous in 1, shiny and dark-green in most populations, olive-green in some, golden-brown in 1, ± smooth to sparsely papillose distally, papillae low and rounded; in transverse section 2-3 rows ventral cells, begleiters undifferentiated, 2-3 rows stereids. Upper laminal cells 9-18 µm wide, 9-23 µm long with 3-5 papillae per cell, some indistinctly "c"-shaped; upper marginal cells 14 µm wide, 8-12 µm long; transitional cells smooth somewhat above basal cells on both surfaces, papillae as on upper cells; basal laminal cells 14-90 µm long, 12-18 µm wide, in small, inconspicuous group, transverse walls yellowish to orange, porose or entire, longitudinal walls hyaline to yellowish, porose or entire, superficial walls smooth, irregularly ± perforated to entire; basal marginal cells distinctly differentiated, in 12-20 rows. Goniautoicous. Perichaetial leaves ± broadly ovate and sheath-like below, abruptly narrowed to oblong upper portion, apex abruptly narrowed to hair-point; perigonial leaves broadly ovate and sheath-like, abruptly narrowed to broadly acute apex, 1.0-1.2 mm long; perigonial paraphyses with upper cell walls sparsely papillose with low, rounded papillae, a few with upper walls thin and ± collapsed.

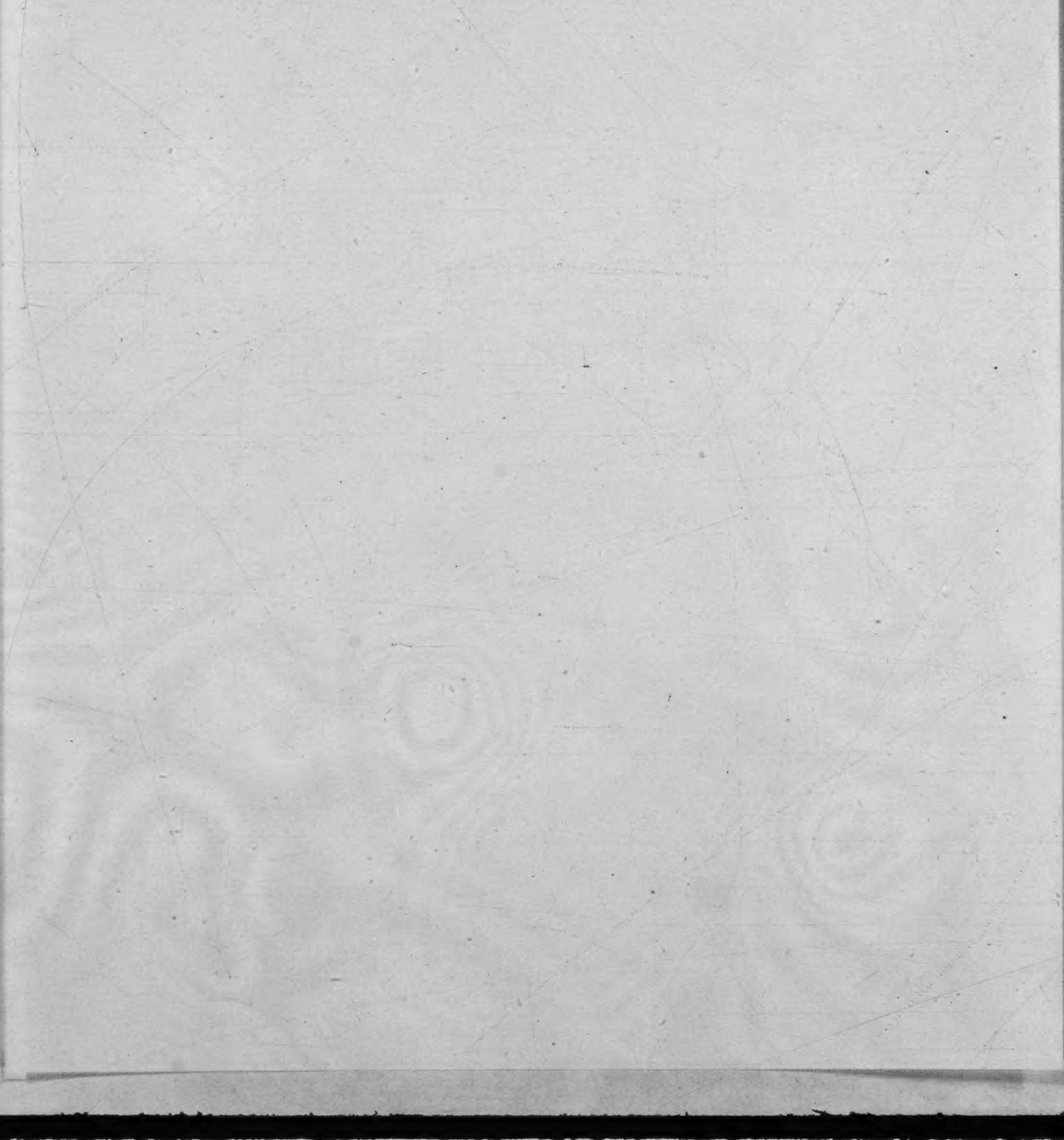
Seta 1-3 mm long, flexuose to erect, strongly ridged and ± twisted dextrorsely, shiny and yellow below, crimson-red distally, dull-orange when older; in transverse section 185-195 µm in diameter. Capsule 1.1-3.0 mm long, when dry cylindric and ± constricted just below mouth, some ± tapered basipetally, others slightly inflated and ± abruptly narrowed to seta, smooth and ± turgid, golden to orange below with crimson-red rim, when old ± puckered and collapsed, dull-orange throughout; exothecial cells 55-85 µm long, 20 µm wide, in transverse section superficial and adjacent radial walls strongly thickened, 14 μm thick; rim cells in 3–6 ± regular rows longitudinally, rather irregular transversely, upper part of each cell rounded and overlapping cell above, 16–30 μm long, 12–18 μm wide, walls very strongly thickened and dark-orange, uppermost row pale orange; stomata superficial, 15–20, scattered, 32–60 μm long, 30–37 μm wide. Peristome absent. Operculum plane-concave and short-rostrate, 0.8 mm long. Annulus undifferentiated. Spores brown, paraisopolar, ± uniform in size in individual capsules in virtually all populations, in 1 highly variable, in polar view radially symmetric and circular, 37–51 μm, in equatorial view polarly asymmetric and concave-convex 37–51 μm X 30 μm, proximal surface verrucate centrally and verrucate-rugulate radially, verrucae 2–5 μm in diameter, smooth, surface finely punctate between verrucae; distal surface verrucate-rugulate, verrucae 2–5 μm in diameter, smooth, surface finely ± punctate between verrucae. Calyptra 2.3–5.0 mm, extends well below capsule, short elliptic-cylindric and ± distinctly contracted to very short, erect or slightly curved rostrum that is 0.5–1.2 mm long, cylinder slightly and distinctly constricted at base or with slight horizontal expansion, fringed, segments ± regularly trapezoidal, 0.4 mm long, broken off in many, golden, to ± dark-brown distally with golden to white fringe, shiny and ± opaque in most populations, somewhat transluscent in very few, smooth to ± papillose throughout, papillae low and rounded, denser and more prominent distally; in transverse section cylinder with 2–3 rows very thick-walled cells, fringe with 1 row of cells, walls exceptionally thickened; in superficial view fringe cells short- to long-oblong. Chromosome number unreported.

Habitat. Plants of E. brevipes most frequently occur intermixed with those of E. brevicolla. As with E. brevicolla, populations of E. brevipes occur in a wide variety of montane habitats including ledges and crevices of rock outcrops from the montane zone to well above timberline, as well as on soil in exposed tundra habitats. The only slight difference apparent between the habitats of these two species is that E. brevipes may tolerate more mesic habitats than E. brevicolla, as plants of E. brevipes are occasionally found in seeps on cliffs associated with Blepharostoma trichophyllum (L.) Dum. and E. alpina. Also, it appears that E. brevipes is restricted to montane habitats, while E. brevicolla is also found in arctic tundra habitats outside of montane regions. However, this may reflect historical factors more than habitat differences.

The fundamental similarity that the association of *E. brevipes* and *E. brevicolla* reflects is the substrate-type of the habitat. Both are rather pronounced siliciphiles. In western North America, the pH of soil samples collected with populations of *E. brevipes* ranged from 5.0 to 6.3 (n=21 from 12 different localities) with a mean of 5.7 (s.d.=±0.49) (Fig. 300). The concentrations of Mg^{++} were about the same as in samples taken with *E. brevicolla*, while the Ca^{++} concentrations were even lower (Figs. 301-302, Table 9). *Encalypta brevipes* is also frequently associated with *E. ciliata* throughout its range and in one collection it is intermixed with *E. microstoma*. Both *E. ciliata* and *E. microstoma* are characteristically associated with acidic substrates, although both are probably tolerant of slightly calcareous conditions as well. Other species associated with *E. brevipes* that reflect this preference for acidic substrates include *Amphidium lapponicum* (Hedw.) Schimp., *Anastrophyllum assimile* (Mitt.) Steph., *Bartramia ithyphylla* Brid., *Cnestrum schisti* (Wahlenb.) Hag., *Isopterygium elegans* (Brid.) Lindb., *Lophozia lycopodioides* (Wallr.) Cogn., *Rhacomitrium lanuginosum* (Hedw.) Brid. and *Tritomaria quinquedentata* (Huds.) Buch. Species with a broader range with regard to substrate-type that are also rather frequently associated with *E. brevipes* include *Bryoerythrophyllum recurvirostrum* (Hedw.) Chen, *Eurhynchium pulchellum* (Hedw.) Jenn., *Pohlia cruda* (Hedw.) Lindb. and *Timmia austriaca* Hedw.

Distribution: The world-wide distribution of *E. brevipes* is a disjointed one with records from rather widely disjunct localities (Fig. 188). In North America, it is known only from the Western Cordillera. Sporadic localities are reported from Alaska in the Brooks and Alaska Ranges; from the Yukon Territory in the Ogilvie, Selwyn and Coast Mountains; and from northwest British Columbia in the Cassiar Mountains. At present, *E. brevipes* appears to be disjunct from these northerly localities to the Rockies in western Alberta and the Coast Range in northwestern Oregon (Fig. 189). Elsewhere, single collectios are reported from southwestern Iceland, the Chibiny Mountains on the Kola Peninsula (Schljakov (1951) - indicated on Fig. 188 by an open circle because the specimen requested from LE has not been made availble to me), the Alps in southeastern France, the High Tatras in Czechoslovakia and the Eastern Sayan Mountains in the Lake Baykal region of Asia (Fig.

Figure 188. Distribution of *Encalypta brevipes*.



WORLD, NORTHERN HEMISPHERE

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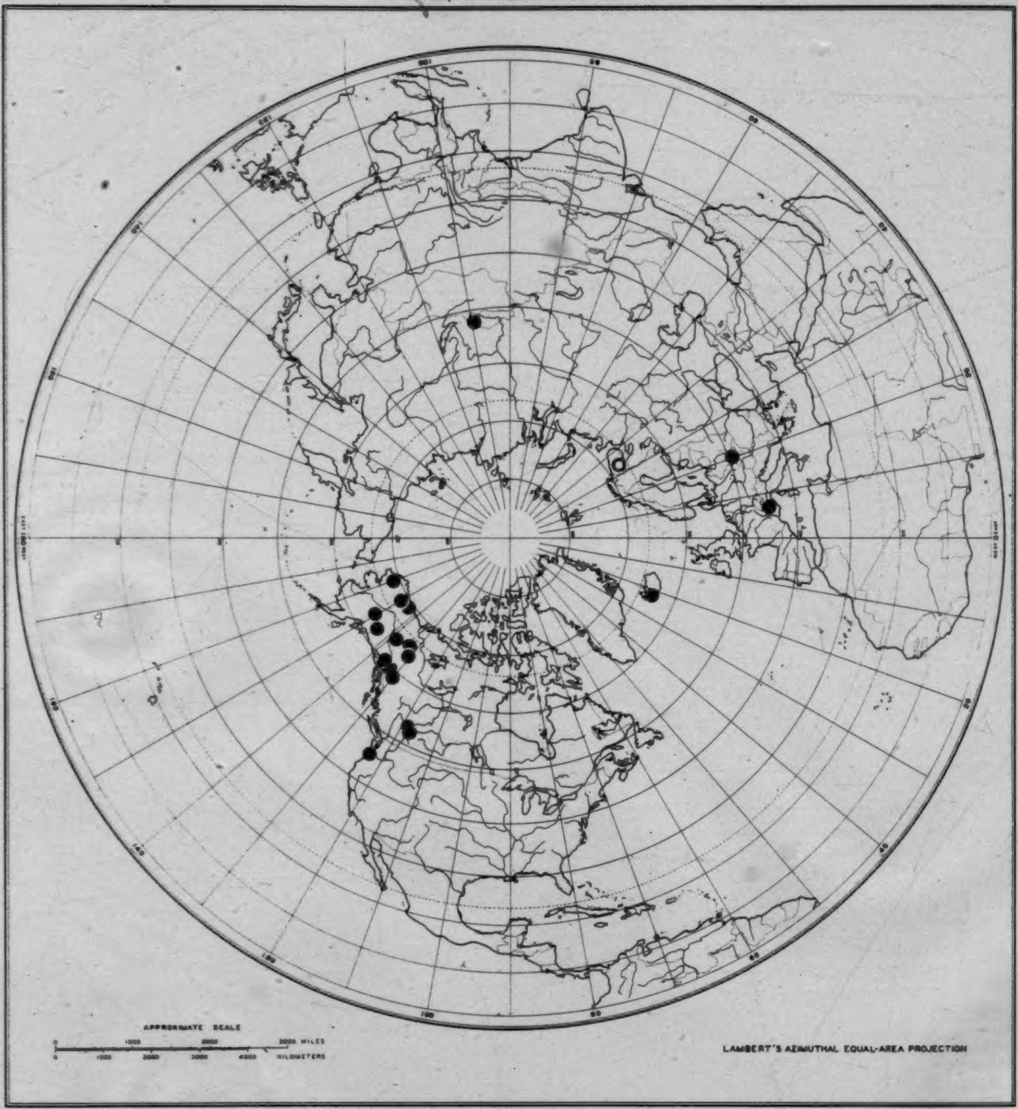
APPROXIMATE SCALE
0 1000 2000 3000 MILES
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LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION

GOODE'S SERIES OF BASE MAPS
HENRY M. LEPPARD, EDITOR

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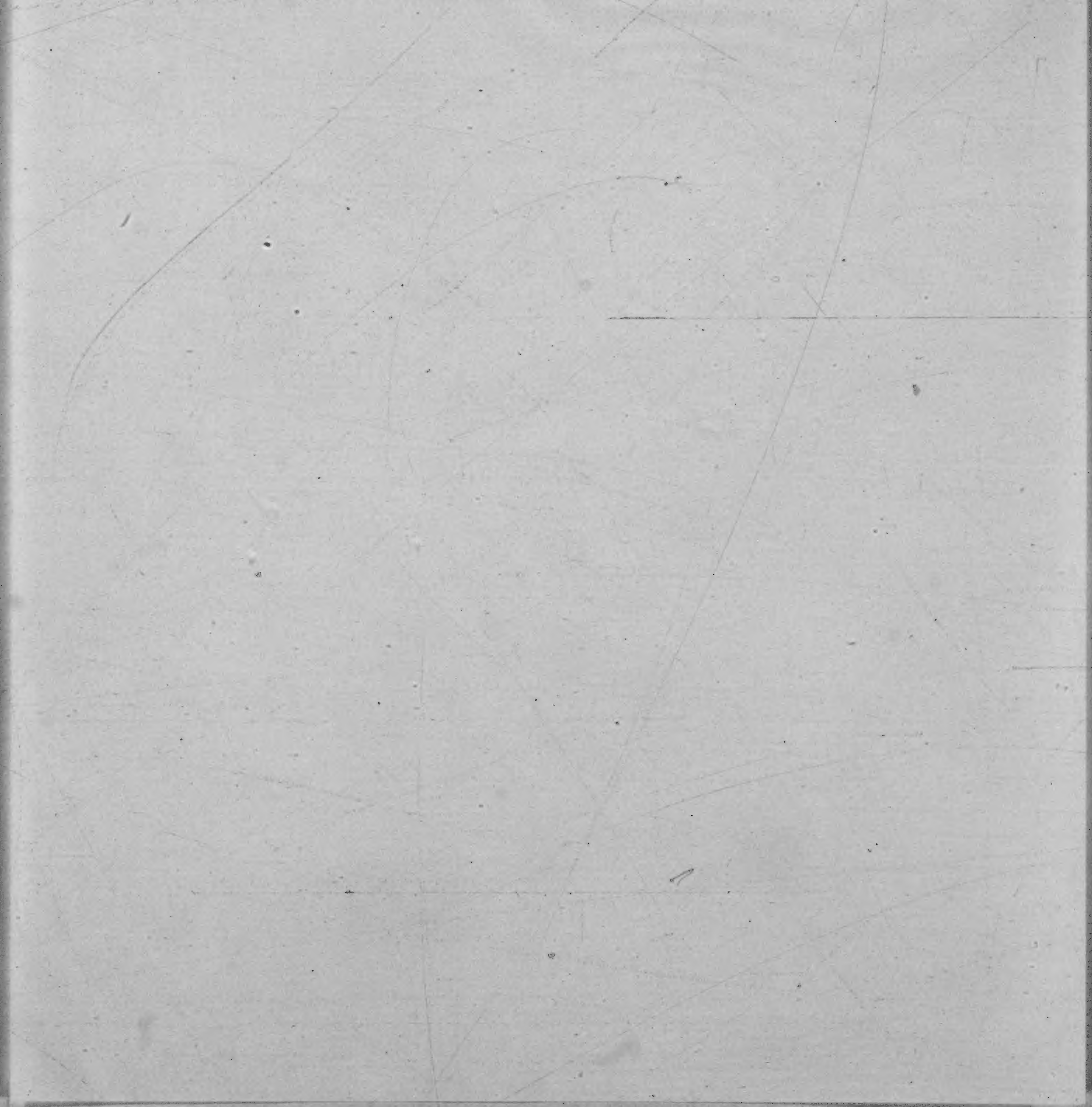
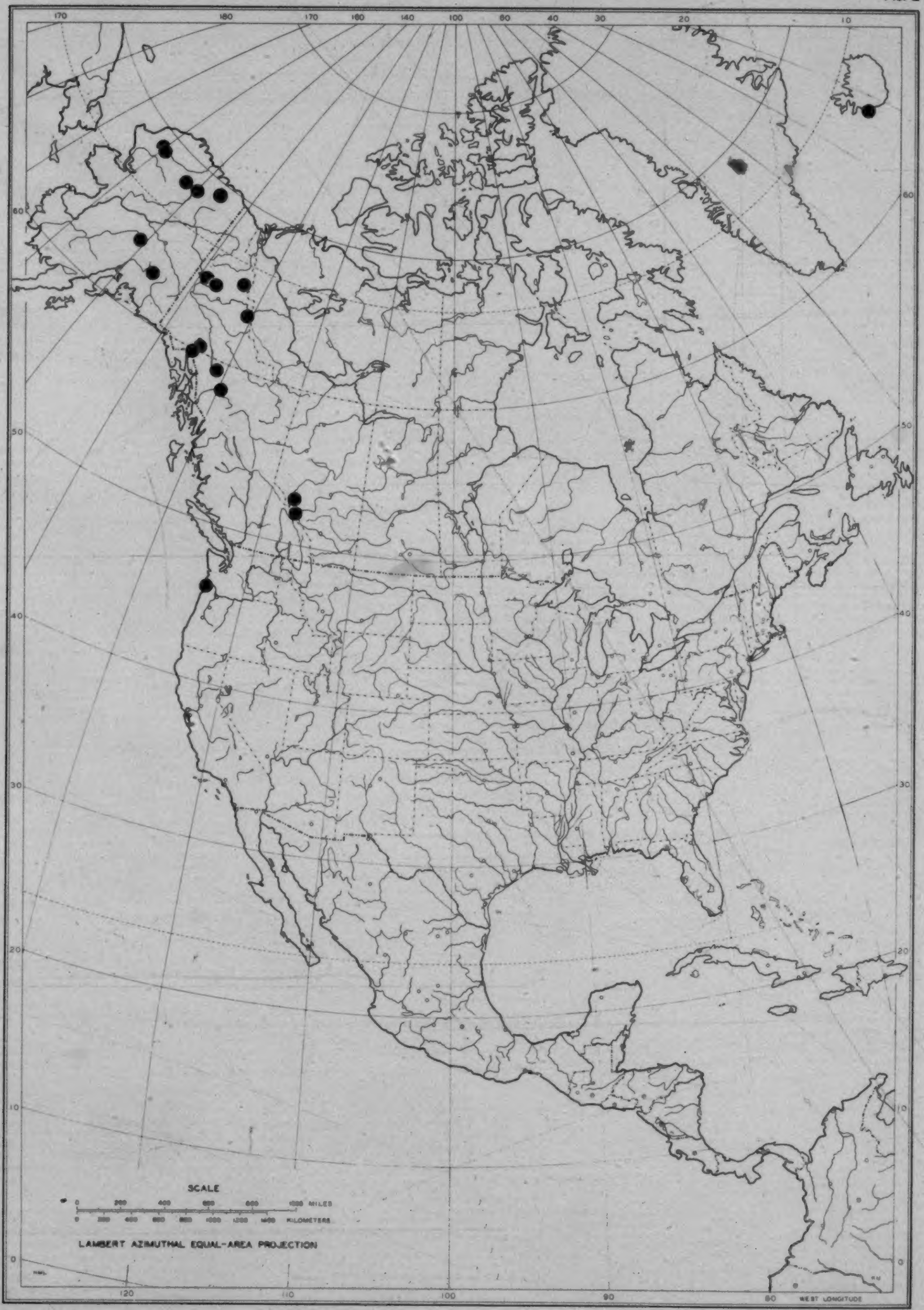
Figure 189. Distribution of *Encalypta brevipes* in North America.



NORTH AMERICA

No. 2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0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
120
110
100
90
80
WEST LONGITUDE

GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

Prepared by Henry M. Leppard
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188).

Within its range in western North America, E. brevipes is a rare species, particularly in the southern Canadian Rockies of western Alberta. Here, it is known from only three different localities, although it has been specifically sought after at a number of other localities in appropriate habitats. Populations of E. brevipes are of slightly more frequent occurrence farther north; however, only one or two consisting of more than a few small tufts of plants have ever been found. Plants of E. brevipes are generally intermixed with other species of Encalypta (as noted above), and the other species are characteristically the more abundant component at any given locality. Beyond the North American continent, E. brevipes appears not only to be extremely rare, but also the specimens observed by me (the holotype collection from the Kola Peninsula is the only one that I have been unable to examine) consist of only a very few plants.

When E. brevipes was reported new to North America (Horton & Murray 1976) from the single Yukon locality and three Alaskan localities, all within the unglaciated areas of Beringia, it was suggested that the distribution of E. brevipes is relictual. Further Alaskan and Yukon localities, as well as records from northern British Columbia and western Alberta were reported by Horton (1979a). At this time, the importance of substrate in determining the occurrence of E. brevipes was stressed, but the original hypothesis of a relictual status was reaffirmed. Recently, the Icelandic and three, widespread Eurasian localities have been recorded (Horton 1980) and were considered to lend further weight to the supposition that populations of E. brevipes were previously more continuously distributed.

Such a scattered distribution pattern as that of E. brevipes can be cited as evidence of long-distance dispersal or as a classic example of a relictual distribution. I believe that there is good evidence to support the latter hypothesis in this particular instance. Hultén (1937) was one of the first to draw attention to the significance, with respect to plant distributions, of the large areas of Alaska-Yukon that were unglaciated during Pleistocene times. More recently, Packer and Vitt (1974) suggested that disjunctions of plants from northwestern North America to the Mountain Park area and other nearby localities in western Alberta suggested that such plants had survived in situ in refugia within glaciated territory. Some apparent disjunctions are now known to have reflected disjunct collecting localities and the patterns have proven to be more-or-less continuous; therefore, the Mountain Park theory was recently evaluated (Horton 1981a). The fact that there are still such plants as *E. brevipes* that are rare and have a sporadic distribution in the Canadian Rockies was cited in support of the original theory, although it was noted that present geological concepts of Cordilleran glaciation suggest that most refugia within glaciated territory probably were not static and did not remain in one place throughout glacial times, as had been implied previously. It appears that the populations of *E. brevipes* that formerly existed south of the unglaciated territory in Alaska-Yukon were considerably reduced during or as a result of the Wisconsinan glaciations. All that is left are a few remnants that have apparently had little success in extending their range. Similarly, the widely disjunct Eurasian and Icelandic populations are probably also the remnants of formerly more frequently occurring populations. If the widely disjunct populations of *E. brevipes* were scattered as a result of long-distance dispersal, it would seem plausible to expect that in one area or another the species might have flourished and extended its range. Yet the Icelandic and each of the Eurasian collections of *E. brevipes* is depauperate and consists of only a few plants, which suggests a stenotypic species that is genetically depleted.

The number of different localities that *E. brevipes* is known from in different parts of its range illustrates the floristic richness of the Canadian Cordillera by comparison to any other Northern Hemisphere montane region, perhaps excepting some areas in Asia about which little information is available. This is also apparent with such other rare species of *Encalypta* as *E. brevicolla* and *E. mutica*. Not only do we have here in western Canada a unique opportunity to examine a relatively undisturbed montane flora in relation to the effects of Wisconsinan glaciation, but as a result of the vagaries of such historical factors, we also appear to have a flora that is unparalleled in its wealth of rare species.

Variation: In spite of the widely disjunct pattern of distribution, the populations of *E. brevipes* are remarkably uniform in structure with the exception of the population from Oregon (*Schofield & J. & G. Godfrey 68029* - UBC), which is differentiated in several structural details. The leaves are much narrower than in all other populations and the costa is golden-brown in color, strongly protruding and almost as broad at the leaf apex as it is basally (Fig. 181). Other populations of *E. brevipes* are characterized by a costa that narrows somewhat distally (Fig. 179), does not protrude strongly above the leaf laminae on the abaxial surface, and is dark-green to olive-green in color. Also, this Oregon population is characterized by an atypical range of variation in spore size, from 37 to 51 μm within individual capsules. In other populations, spore size is more-or-less uniform. At the present time, I feel that it is inappropriate on the basis of this single population to give nomenclatural recognition to these differences. It should be noted that the population of *E. brevicolla*, also disjunct in Oregon, is similarly atypical with structural differences in the peristome and the calyptra (see discussion of Variation under *E. brevicolla*). On the basis of the data presently available, it is difficult to assess whether the character-states that differentiate these two populations reflect genetic isolation or if they are responses to different environmental conditions unique to this particular region.

Phylogenetic Relationships: *Encalypta brevipes* appears to be most closely related to *E. brevicolla* (see discussion under Phylogenetic Relationships of *E. brevicolla*) and also to *E. ciliata*. Features that link *E. brevipes* with *E. ciliata* include the fringed calyptra that is smooth in some populations, the smooth, turgid capsule that is broadly cylindric with numerous, scattered stomata, the yellow seta that is crimson-red distally, and the leaves with a basal marginal border. Also, the spores are finely more-or-less punctate as are those of *E. ciliata*, although the macro-ornamentation is quite different. *Encalypta brevipes* is markedly divergent from both *E. brevicolla* and *E. ciliata* in the characteristic of a short-rostrate calyptra.

Specimens Examined: ALA (8), ALTA (60), G (1), Priv. Herb. D. G. Horton (25), IRK (1), NY (2), PRC (1), UBC (2).

ENCALYPTA CILIATA Hedwig,

Spec. Musc. 61. 1801.

Figs. 2, 16–17, 39, 50–51, 61–62, 64, 68–69, 190–216.

Type: None cited; reference made to previous publications. (Lectotype: "Leersia ciliata" G-DC.(in part)!).

Encalypta fimbriata Lam. *et* DC., Fl. Franc. 2: 453. 1805. *Nom. illeg. incl. spec. prior.*

Encalypta ciliata Hedw. var. *concolor* Hook. *et* Tayl., Musc. Brit. 35. 1818. *Nom. illeg. incl. typ. spec.*

Encalypta mexicana C. Müll., Syn. 1: 516. 1849. Type: "Mexico: C. Ehrenberg." (Lectotype: "Encalypta leptodon mihi n.sp. Trachythole im Krater des Cerro de las Nabajas Martio leg. C. Ehrenberg Schlechtendal nr. 62." BM-Schimp.!).

Encalypta ciliata var. *microstoma* Schimp., Coroll. 38. 1856. Type: None cited. There is no specimen in Schimper's herbarium in BM; therefore, a neotype should be selected.

Encalypta coarctata Mitt., J. Linn. Soc. Bot. 12: 181. 1869. Type: "Andes Quitenses, in summo monte Pichincha (10,000 ped.), *Jameson*." (Holotype: "Encalypta ciliata var. Snowy summit of Pichincha Jameson" NY-Mitt.!; Isotypes: BM-Hook.!, BM-Shuttleworth!, BM (two specimens)!, FH-Tayl.!, G-Boissier!; Possible Isotypes: BM-Hook.!, NY-Mitt.!).

Encalypta laciniata (Hedw. *ex* Lindb.) Lindb., Act. Soc. Sci. Fenn. 10: 18. 1871.

Leersia laciniata Hedw. *ex* Lindb., Musci Scand. 20. 1879. *Nom. illeg. incl. spec. prior.*

Leersia borealis Kindb., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 7(9): 128. 1883. Type: "N." (Thör-Björn Engelmark has informed me (*in litt.*) that there is no specimen in S).

Encalypta ciliata Hedw. var. *gymnostoma* Bruch *ex* Husn., Musc. Gall. 198, pl. 53, fig. 6. 1888. *Nom. illeg. incl. var. prior.*

Encalypta alaskana Kindb. *in* Macoun *et* Kindb., Cat. Canad. Pl. 6: 269. 1892. Type: "Mixed with a *Bryum* on earth, Ounalaska Island, Behring Sea, August 21st, 1891. (J. M. Macoun.)" (Holotype: "N. Amer., Alaska, Ounalaska 21/8 91 J. M. Macoun" S-Kindb.!).

Encalypta breviseta C. Müll., Nuovo Giorn. Bot. Ital. n.s. 3(1): 103. 1896. Type: "In medio monte Kuan-tou-san." (Lectotype: "No. 1040 In monte Kuan-tou-san prov. Schensi. Giraldi Jul. 1894 determinavit C. Müll." FI-Levier!; Syntypes: FI-Levier!, H-Br!).

Encalypta erythrodonta C. Müll., Nuovo Giorn. Bot. Ital. n.s. 5(2): 172. 1898. Types: "China interior, prov. Schen-si sept., in monte Tui-kio-san et in monte Kuan-tou-san, Oct. et Nov. 1896: *J. Giraldi*." (Lectotype: "China interior, provincia Schen-si sept. in monte Kuan-tou-san 5 Nov. 1896 Giraldi" FI-Levier (in part)!).

Encalypta aristatula C. Müll., Gen. Musc. Fr. 381. 1900. *Nom. nud.* Specimen cited by Müller: "Im nordwestlichen Himalaya sammelte C. G. Rogers bei 11,000 F. Höhe E. aristatula n. sp. als Gegensatz zu E. ciliata." (BM!, FI-Levier (2 specimens)!, H-Br!, M!, PC-Cardot!, PC!, S-Dusen).

Encalypta austrociliata Broth. *in* Dus., Ark. Bot. 6(8): 30, pl. 12, figs. 1-6. 1906. Types: "Patagonia australis ad lac. Lago Argentino in rupibus rivalibus; ad lac. Lago San Martin in fageto ad saxa rivalia." (Lectotype: "Patagonia australis Lago Argentino in rupibus rivalibus" S-Dusen!, Isotype: H-Br!; Syntypes: S-Dusen!, H-Br!, S-Möller!, PC-Card.!).

Encalypta leiotheca Herz., Biblioth. Bot. 87: 51. 1916. Type: "Unter Rasenwurzeln bei der Abra de San Benito, ca. 3800 m, No. 4353." (Lectotype: "Plantae in itinere secundo per Boliviam lectae No. 4353 Encalypta leiotheca H. *n.sp.* Unter Rasenwurzeln bei der Abra de San Benito ca. 3800 m leg. Th. Herzog Juni 1911" JE-Herz.!; Isotypes: BM!, H-Br!, M!, S-Froehlich!, S-Regnell!, W!).

Encalypta leiocarpa Herz. *ex* Broth., Nat. Pfl. ed. 2, 10: 242. 1924. *Err. pro E. leiotheca* Herz.

Encalypta scabrata Bartr., Bernice P. Bishop Mus. Bull. 101: 72. 1933. Type: "rock crevices below Rest House, Haleakala, Maui, altitude 8,800 feet, February 14-15, 1930, St. John, number 580-a." (Lectotype: "No. 580 Encalypta scabrata Bartr. sp. nov. rock crevices below Rest House, Haleakala, Maui, Elev. ca. 8800 ft. leg. H. St. John. Feb. 14-15 - 1930." FH-Bartram!; Isotypes: BISH!, NY!, S!; Paratypes: BISH (2 specimens)!, BM-Hook.!, NY (2 specimens)!).

Encalypta ciliata Hedw. subsp. *eu-ciliata* Giac., Ist. Bot. Reale Lab. Crittog. Pavia Atti ser. 5, 4: 199. 1947. *Nom. illeg.*

Nomenclatural Notes: (1) That there may be problems with typification of species described by Hedwig has been discussed by Florschütz (1960), Margadant (1968), and most recently by Koponen (1979) and Vitt (1980a). The first description of E. ciliata, that can be considered as valid in accordance with Article 13.1 of the ICBN (Stafleu et al. 1978), is in Hedwig's (1801) Species Muscorum Frondosorum. However, there are no specimens cited, only a general description of habitat. Florschütz (1960) noted that specimens often were not cited, particularly for European species. Instead, in the case of E. ciliata as with many other species, Hedwig referred to a number of earlier descriptions and illustrations including those in Dillenius' Historia Muscorum (1768). Encalypta ciliata is not figured in Species Muscorum, and, the first reference is to the description and illustration in Hedwig's Stirpes cryptogamiacae..., which was later published as the Descriptio et adumbratio microscopico-analytica muscorum frondosorum (1787-1797) (cf. Margadant 1968). I would agree with Vitt (1980a) that "...typification of a Hedwig name should be from a specimen in Hedwig's herbarium (if present) rather than from a Dillenian specimen which Hedwig cited in the protologue.". There is one specimen in the Hedwig-Schwaegrichen herbarium in G with Hedwig's handwriting on it. The label information is "Enc. ciliata St. Crypt. 1 p. 49 t. 19", but neither of the two plants on this sheet match any of the plants illustrated in Hedwig's Descriptio. In the De Candolle herbarium (also in G), which contains some Hedwig specimens (cf. Florschütz 1960), there is another specimen with "Leersia ciliata" written on it by Hedwig. This specimen consists of a mixture of one plant of E. ciliata and another of E. streptocarpa. Peterson (1977), Koponen (1979) and Shaw (1980) have cited other examples in which Hedwig's original specimens consisted of mixed collections. In the present instance, the plant of E. ciliata is almost certainly the one figured in the upper left-hand corner of Plate 19 in the Descriptio et adumbratio... (Fig.), although two of the capsules and the lower right-hand innovation have been broken off (Fig.). Therefore, I have selected this plant as the lectotype of E. ciliata.

(2) Pekka Isoviita has kindly informed me (in litt.) that there is a letter (dated May 19th, 1906) in Helsinki University Library from Per Dusen thanking Brotherus for the description of E. austrociliata. Therefore, Brotherus is considered to be the author of the description and the citation is E. austrociliata Broth. in Dusen, rather than E. austrociliata Broth. ex Dusen.

(3) The striking resemblance of some species of *Tortula* to *E. ciliata* is exemplified by the fact that Carl Müller (1896) described a *Tortula* species as *E. breviseta* var. *medioseta*. In a publication based upon collections made by Giraldi in the Himalayas of China, Müller described two taxa of *Encalypta* consecutively. The first of these is *E. breviseta* and a locality is cited. Under the description of the second, *E. breviseta* var. *medioseta*, there is no direct citation of a locality, but rather the notation "Inter priorem speciem crescens.". The specimens that Müller described were sent to him by Levier. The type specimens of *E. breviseta* in Levier's herbarium are all *E. ciliata*; one of the types of *E. breviseta* var. *medioseta* is a mixture of *E. ciliata* and a *Tortula* species. The most apparent differences between the plants of the *Tortula* species and those of *E. ciliata* are the longer, apiculate apices of the leaves and the slightly longer seta of the former. These features correspond very well to Müller's description of *E. breviseta* var. *medioseta*: "...pedunculo parum longiore, foliis rotundato-acuminatis longipilis majoribus." (the comparison of seta length is with reference to *E. breviseta*). Therefore, it seems that Müller was sent a mixed collection consisting of *E. ciliata*, which he had already described from a different collection as *E. breviseta*, and a *Tortula* species which he described as *E. breviseta* var. *medioseta*. To do Müller justice, in vegetative features the *Tortula* species is virtually indistinguishable from *E. ciliata*.

Diagnosis and Differentiation: Throughout the greater part of its range in the Northern Hemisphere, *E. ciliata* is a narrowly defined species in structural features. Among the most distinctive of these is the calyptra. It consists of a long, narrow and well-defined rostrum, a relatively short cylinder, and a precisely segmented fringe that is pendent to more-or-less flaring from a narrow, horizontal and distinctly-defined ridge at the base of the cylinder. Few collections of *E. ciliata* in the herbaria that I have examined are misdetermined, and I believe that it is the unmistakably fringed calyptra that so many bryologists are readily able to associate with this species. Even when the fringe is broken off, which is by no means uncommon, the narrow, horizontal ridge at the base of the cylinder persists and is a good differentiating feature. Also, the length of the rostrum is strikingly long in relation to the length of the cylinder; generally, the ratio is equal to or greater than 1:1.5. a long, narrow and well-defined rostrum, a generally, the ratio is equal to or greater than 1:1.5. Also characteristic are the perfectly smooth, turgid-appearing capsules that are cylindric and strongly constricted just below the mouth. There is a well-developed, single peristome of lanceolate teeth (more-or-less "aberrant" capsules, the more extreme expressions of which are characterized by a very small mouth and irregular peristome of narrower, linear teeth, occur quite frequently in populations of E. ciliata; see Diagnosis and Differentiation under E. microstoma). The seta is strongly dextrorsely twisted just below the capsule. The broad, mucronate leaves have a prominent costa and the margins are narrowly recurved basipetally from the mid-portion. Also, the leaves are very dense and the stems are much-branched giving the plants a very luxuriant appearance. Microscopically, E. ciliata is defined by leaves with a costa that is smooth and shiny on the abaxial surface. There is a distinct basal marginal border and the basal cells are well-defined with the transverse walls dark-orange and the longitudinal walls hyaline. The papillae on the abaxial surface of the transitional cells extend to the basal cells. Spores are heteropolar with the proximal surface defined by a distinct trilete mark and numerous radial plicae. Structure of the distal surface is quite variable, but the entire surface of the spore is more-or-less distinctly and finely pitted; however, in some this is visible only with the SEM.

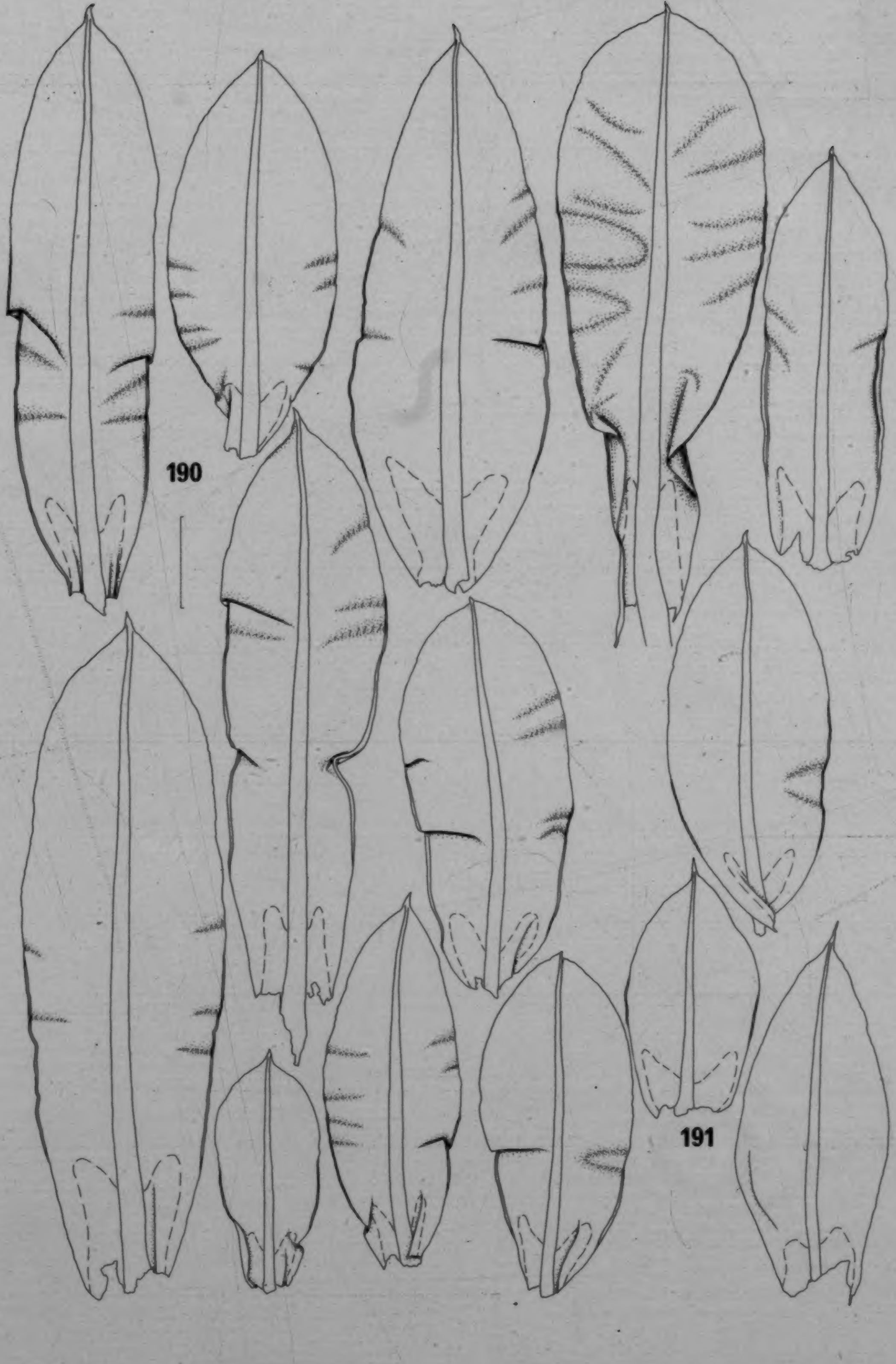
Coloration is in itself an important differentiating feature of E. ciliata. The orange or yellow tones so characteristic for this species are quite striking and generally are immediately apparent upon cursory inspection, even without the aid of a microscope. The shiny calyptra is pale-golden and more-or-less transluscent; however, in some populations the calyptra fringe is pale brown and in others the whole calyptra is darker colored; mature capsules are copper- to rust-colored, while younger ones are greenish-yellow to yellow, the peristome is dark-orange; the seta is yellow; and the shiny, yellow to golden-brown costa forms a prominent keel on the olive-green leaves.

Encalypta ciliata might be confused with several closely related species including E. affinis, E. brevicolla, E. brevipes and E. microstoma. The calyptra of E. affinis consists of a longer cylinder that is less distinctly narrowed to the rostrum and there is only a slight constriction at the base just above the fringe, or a very poorly defined extension that is quite different from the sharp ridge that characterizes E. ciliata. Also, the calyptra of E. affinis is opaque and dull golden-brown owing to the finely papillose outer surface.

Figures 190-191. Encalypta ciliata. Scale=1 mm.

Fig. 190. Vegetative leaves.

Fig. 191. Perichaetial leaves.



190

191

Capsules are pale-golden in color with a narrow, bright-red rim and there is only a slight constriction just below the mouth. The peristome is pink and the lanceolate-linear teeth are longer than those of *E. ciliata*. Leaves of *E. affinis* are quite different in the characteristic dark-brown overtones, and the costa is densely papillose on the abaxial surface and therefore dull. *Encalypta affinis* is readily differentiated from *E. ciliata* by the papillae on the abaxial surface of the basal leaf cells. These are most prominent along the margins. Also, a basal marginal leaf border is virtually undifferentiated in *E. affinis* and the marginal cell walls are colored as those of the basal laminal cells. The abaxial surface of the costa is densely papillose in the region of the transitional cells and the papillae on the abaxial surface of the transitional cells are much larger than those that characterize *E. ciliata*. In *E. ciliata* the papillae of the transitional cells are undifferentiated from those on the upper cells. Spores of *E. affinis* are small and indistinctly polar with the surface covered by relatively small gemmae.

The white peristome of *E. brevicolla* is one of the most striking features that differentiates it from *E. ciliata*. Also, *E. brevicolla* is characterized by a calyptra very similar to that of *E. affinis* and therefore quite different from that of *E. ciliata* in a number of features, as discussed above. Capsules of *E. brevicolla* are brownish below and grade to crimson-red with a distinctive irridescent sheen in the upper part. The seta is dark-red. There is a blackish coloration to the leaves, which are hair-pointed and have plane margins. *Encalypta brevicolla* is difficult to differentiate from *E. ciliata* on the basis of microscopic leaf character-states. However, the coloration of the basal laminal cells is somewhat different. In *E. brevicolla* both the transverse and the longitudinal walls are dark-orange. Also, the abaxial surface of the costa is densely papillose in the region of the transitional cells. Spores of *E. brevicolla* are quite different in the rather large, warty protuberances that more-or-less cover the surface. Also, there is no trilete mark or it is indistinct.

When calyptrae are present, the short, stubby rostrum of *E. brevipes* is enough to differentiate this species from *E. ciliata*. In shape, capsules of *E. brevipes* are more-or-less identical to those of *E. ciliata*, but there is never any trace of a peristome in *E. brevipes*. *Encalypta brevipes* is characterized by a strikingly short seta and leaves with long hair-points; the latter is a particularly reliable feature for separating this species from *E. ciliata*. As with *E. brevicolla*, *E. brevipes* can be differentiated by the blackish tones of the plants and the plane leaf margins. Microscopically, the marginal border at the base of the leaves is somewhat broader in *E. brevipes* than in *E. ciliata*, but *E. brevipes* is better differentiated by the generally pale coloration of the transverse walls of the basal cells. The spores of *E. brevipes* are indistinctly polar and there is no trilete mark visible.

Encalypta microstoma is very close to *E. ciliata* structurally. The most readily apparent features that distinguish *E. microstoma* are the muticous leaves with plane margins and the dark-brown fringe of the calyptra. More subtle differences are discussed under Diagnosis and Differentiation of *E. microstoma*

Some species of *Tortula* and *Desmatodon* bear a rather striking, superficial resemblance to *E. ciliata*. For example, the broad leaves of *T. mucronifolia* Schwaegr. with revolute margins and a mucronate apex parallel those of *E. ciliata*. However, the upper laminal cells of *T. mucronifolia* are less papillose than those of *E. ciliata* (smooth in some populations); therefore, they appear less dense, and the basal cells lack the colored walls that are so distinct in *E. ciliata*. Also, the sporophyte is quite different in shape with the capsule asymmetric and, when present, the broad basal membrane of the peristome and the cucullate calyptra are good differentiating features. *Desmatodon latifolius* (Hedw.) Brid. is, in some ways, more similar to *E. ciliata* than *Tortula mucronifolia*. The leaves are more densely papillose, as in *E. ciliata*, and the peristome has a low and therefore inconspicuous basal membrane. However, the leaves are generally short hair-pointed; the peristome teeth are relatively long and linear (in this feature *D. latifolius* is more reminiscent of *E. affinis*); and the capsules are glossy and dark-brown. As with *T. mucronifolia*, the definitive feature that differentiates *D. latifolius* from *E. ciliata* as well as all species of *Encalypta*, is the lack of colored walls in the basal cells.

Description: *Plants* to 35 mm tall, olive-green above in most populations to light- or dark-green, few with glaucous sheen, brown below in most populations to blackish; ± branched. *Stem* in transverse section with central strand absent. *Brood bodies* absent. *Axillary hairs* sparse. *Leaves* when dry incurved and irregularly twisted, laminae ± undulate and inflexed; 2.2-6.8 mm long, 0.8-2.0 mm wide, oblong to narrowly elliptic-oblong to obovate-oblong to lingulate, apex acute and mucronate to apiculate, muticous and slightly cucullate in few populations, green, brownish to blackish in few populations; margins narrowly recurved basipetally from mid-portion to region of basal cells, few recurved almost to base, very narrowly recurved or broadly recurved in few populations. Costa excurrent, ends just below apex in few populations, abaxial surface prominently keeled, shiny and yellow to dark-brown, green on uppermost leaves in some populations, sparsely papillose to smooth near base; in transverse section with 2-3 rows ventral cells, begleiters undifferentiated, 2-3 rows stereids. Upper laminal cells (7)12-16(20) μm wide, 9-20(25) μm long, with 3-6 papillae per cell, some indistinctly "c"-shaped; upper marginal cells (12)14-16(18) μm wide, (7)9-12(14) μm long; transitional cells papillose to basal cells on abaxial surface, papillae as on upper cells, on adaxial surface smooth well above basal cells; basal laminal cells 28-110(120) μm long, (11)16-25(30) μm wide, prominent, transverse walls dark-orange, longitudinal walls hyaline, superficial walls smooth, small papillae sparse on upper walls on abaxial surface in few populations, entire to irregularly ± perforated; basal marginal cells distinctly differentiated in 4-6(9) rows. Goniautoicous. Perichaetial leaves sheath-like and broadly obovate-oblong to narrowly elliptic-oblong, apex acute, margins plane in most populations to recurved; perigonial leaves 0.8-1.1 mm long, sheath-like and oblong to elliptic to obovate-oblong, apex acute and muticous to sharply mucronate, margins plane to recurved in upper part; perigonial paraphyses with upper cells entire or divided in 1 or 2, walls smooth.

Seta (1.5)2-10(15) mm long, flexuose to erect, slightly twisted sinistrorsely below, ± strongly twisted dextrorsely near capsule, shiny and yellow to copper- or rust-colored, some red near base of capsule, in very few populations ± red to blackish throughout; in transverse section 140-160 μm in diameter. Capsule 1.2-4.0 mm long, when dry cylindric with abrupt constriction below mouth to cylindric and gradually or abruptly narrowed to small or minute mouth, abruptly contracted and slightly twisted to seta, smooth and ± turgid-looking, yellow to copper- to rust-colored with rim red or undifferentiated in some, when young delicately, longitudinally striate, greenish-yellow with ± red rim; when old slightly wrinkled to delicately longitudinally striate, collapsed, some split from mouth or centrally, dull-orange; exothecial cells 35-140 μm long, 12-35 μm wide, in longitudinal rows, in transverse section walls strongly, ± evenly thickened on outer surface, 6 µm thick; rim cells in (3)4–7(9) ± regular longitudinal rows, (7)9–23(25) µm long, (9)12–20(28) µm wide, walls ± thickened, lower cells slightly overlap cells in row above in few populations; stomata superficial, scattered, 26–46 µm long, 23–35 µm wide. Peristome present and ± well-developed to absent, 0.1–0.2 mm long, in 1 concentric layer, teeth 16, erect to inflexed or slightly reflexed, ± regularly lanceolate to truncate, dark-orange to hyaline or white in few populations, outer surface with 1 vertical row of cell plates, densely striately papillose, striae vertical to slightly oblique, to ± smooth in few populations, inner surface with 2 vertical rows of cell plates basally, smooth and shiny; preperistome present in very few populations, consists of 2 vertical rows of cell plates. Operculum when dry concave-plane to plane-convex to convex and rostrate, in "aberrant" capsules ± narrowly-conic and ± attenuated to rostrum, 0.8–1.7 mm long. Annulus undifferentiated, some "aberrant" capsules cleistocarpous. Spores orange, heteropolar, in polar view radially symmetric and circular (23)28–41 µm, in equatorial view polarly asymmetric and plane-convex, 23–28 µm X (23)28–41 µm, proximal surface with numerous, radial plicae and ± distinct triradiate mark, in some ± irregularly rugose around trilete mark, minutely ± distinctly pitted; distal surface highly variable between and somewhat within populations, 5–7 prominent radial plicae extend from ± distinct rim bordering ± distinct central pit, in some pit, rim and plicae overlain by verrucose reticulum, minutely ± distinctly pitted. Calyptra 2.5–7.0 mm long, extends well below capsule, cylindric to narrowly elliptic-cylindric, narrowly-cylindric in few populations, ± distinctly contracted, indistinctly contracted in few, to curved or erect rostrum that is 1.0–2.3 mm long, base of cylinder slightly and distinctly extended horizontally or obliquely, indistinctly in few, fringed, segments not separated with spear-stage sporophytes, with expanded sporophytes segments broadly to narrowly trapezoidal, appear slightly inflated, pendent to spread, ± broken off with age, calyptra transluscent and golden, some ± brown distally, very few ± brown throughout, in some fringe pale brownish, very few with dark-brown fringe, shiny, very few dull, transluscent, few opaque, smooth, papillose in very few, papillae small and rounded; in transverse section cylinder with 2–3(4) layers of cells with very thick walls, fringe with 1 row of cells, walls exceptionally thickened in 2 layers, outer yellowish, inner hyaline; in superficial view fringe cells short- to long-oblong, bordered above by 2–3 rows ±

quadrate cells. *Chromosome number* n=13 (Anderson & Crum 1958, Smith & Newton 1968).

Habitat Northern Hemisphere populations of *E. ciliata* occur most frequently in forested habitats at lower elevations, although they are found less commonly in tundra habitats as well. This characteristic association with forested habitats differentiates *E. ciliata* from almost all other species of *Encalypta*. Therefore, *E. ciliata* occurs not only in montane and arctic habitats, as is typical of most species in the genus, but it is also widespread in forested regions beyond the mountains. Furthermore, in North America most species of *Encalypta* are more-or-less restricted to continental parts of the Western Cordillera, while popuations of *E. ciliata* are quite common along the West Coast. This may reflect a greater tolerance for conditions of higher humidity. In North America, *E. ciliata* occurs in the temperate rain forest on the West Coast, in the boreal forest across the interior of the Continent, as well as in the prairie in pockets of forest associated with river valleys, and down into northerly portions of the deciduous forest along the East Coast. Similarly, in Europe, *E. ciliata* is found not only in the Alps, but is also widespread in temperate and boreal forest regions to the north and extends down into the more southerly forests that occur in regions around the Mediterranean. Populations of *E. ciliata* from subtropical regions of the Northern Hemisphere, for example Mexico, and Southern Hemisphere populations from South America and Africa are more-or-less restricted to alpine habitats. *Encalypta ciliata* generally grows on soil over rock outcrops that are more-or-less shaded and somewhat mesic. In tundra habitats, *E. ciliata* also grows on soil on the edge of small solifluction terraces or on the edge of frost boils. In these habitats too, the populations are often on slightly seepy soil or in such a position that they will be somewhat protected from desiccation. However, the fact that some populations of *E. ciliata* grow in very exposed habitats may indicate that this species has broad tolerances with respect to shade and exposure.

In western North America, *E. ciliata* has broad tolerances with regard to substrate pH. The pH of soil samples tested ranged from 5.3 to 7.1 (n=50 from 25 different localities), but the mean of 6.3 (s.d.=±0.43) (Fig. 300) indicates a rather marked preference for substrates with a subneutral or slightly acidic pH. The results of analyses of Ca^{++} and

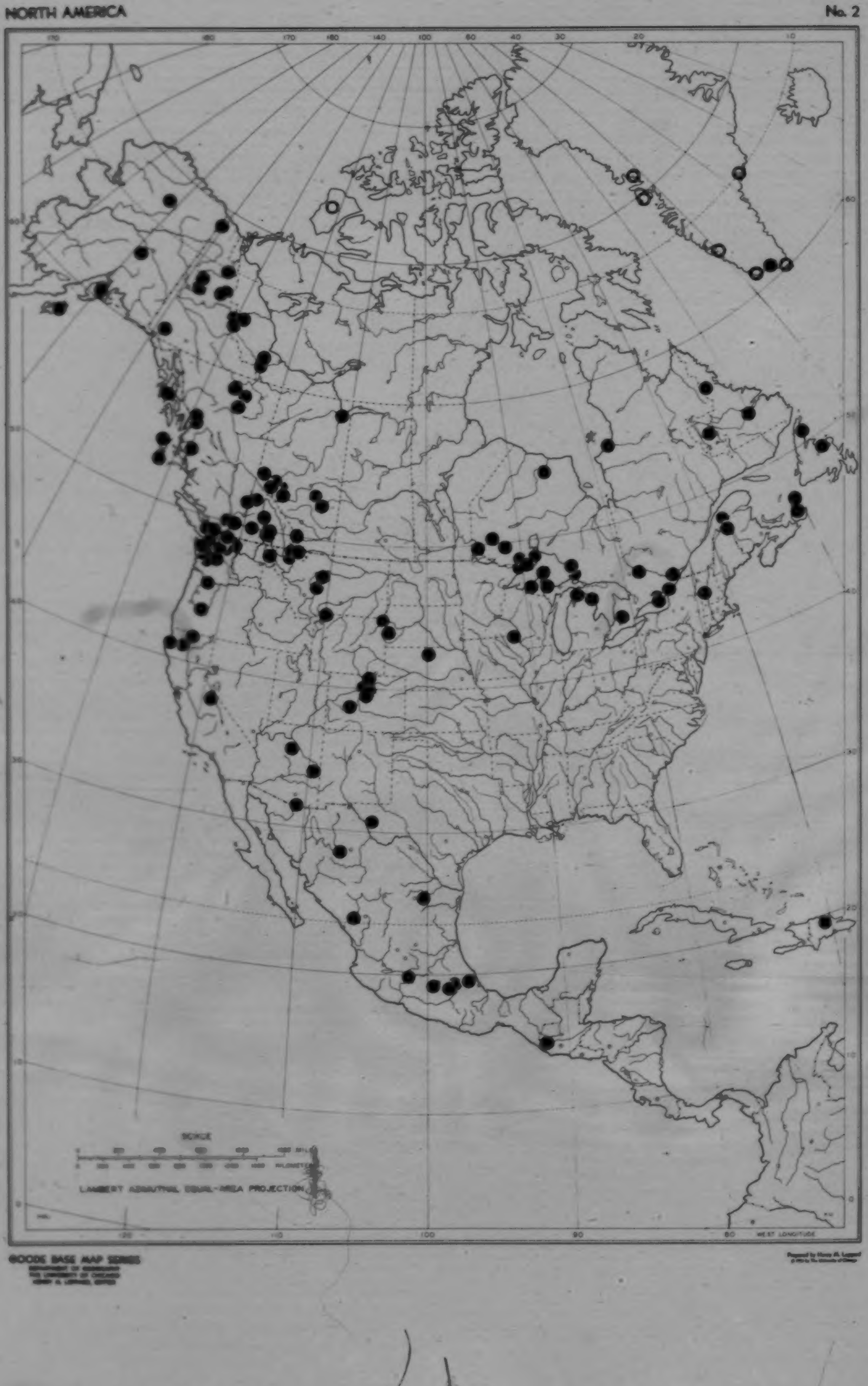
Mg⁺⁺ content of the soil also reflect a tolerance of slightly lower levels than is characteristic of most species (Figs. 301–302, Table 9). Associated species reflect this tolerance of both acidic and calcareous substrates, but these vary somewhat according to regional floristic differences because E. ciliata is so widespread. However, three species that are quite frequently associated with E. ciliata throughout its range in the Northern Hemisphere are Bryoerythrophyllum recurvirostrum (Hedw.) Chen, E. rhaptocarpa and Pohlia cruda (Hedw.) Lindb. On a regional level in North America, species commonly occurring with E. ciliata are, on the West Coast, Amphidium lapponicum (Hedw.) Schimp., Aulacomnium androgynum (Hedw.) Schwaegr., Claopodium whippleanum (Sull.) Ren. et Card. and Isothecium stoloniferum Brid.; in the Rocky Mountains, Brachythecium velutinum (Hedw.) B.S.G., Bryoerythrophyl recurvirostrum, Eurhynchium pulchellum (Hedw.) Jenn., Mnium thomsonii Schimp., Myurella julacea (Schwaegr.) B.S.G., Platydictya jungermannioides (Brid.) Crum and Timmia austriaca Hedw.; in the Midwest and the East, Anomodon attenuatus (Hedw.) Hueb., A. rostratus (Hedw.) Schimp. and Plagiopus oederiana (Sw.)Limpr.; and in Mexico, Amphidium cyathicarpum (Mont.) Broth., Anacolia intertexta (Besch.) Par., Aongstroemia julacea (Hook.) Mitt., Bartramia potosica Mont., Brachythecium corbieri Card., Campylium chrysophyllum (Brid.) J. Lange, Didymodon australasiae (Hook. & Grev.) Zander, Eurhynchium pulchellum, Mielichhoferia sp., Morinia ehrenbergiana (C. Müll.) Ther., Pohlia cruda (Hedw.) Lindb., Polytrichum juniperinum Hedw., Pottia cf. heimii (Hedw.) Hamp., and Tortula cf. princeps De Not.

It appears that the European populations of E. ciliata occur on substrates with a similarly broad range of pH. Brotherus (1923) stated that it is found on weakly calcareous or calcareous-free rocks. In contrast, Mårtensson (1956) stated that in the Torneträsk area of northern Sweden, E. ciliata occurs on calcareous substrata. The general view presented by Limpricht (1890) perfectly parallels what I have found here in North America. He stated that E. ciliata grows "...auf mergeligem und kalkigem Boden...häufig an kalkärmeren Felsen...auch auf kalkfreiem Gestein...selten auf reinem Kalke.".

Distribution: Encalypta ciliata is reported from North America, South America, Eurasia and Africa. In North America, E. ciliata is known from scattered localities in Alaska, the Yukon and extreme western Northwest Territories, as well as on Banks Island in the north, southward along the Western Cordillera as far as Guatemala, but appears to be absent from the Great Basin in Utah, Nevada, southern Idaho and eastern Oregon. In Mexico, one locality is disjunct on Cerro Potosi and most collections are from the central volcanic highlands. *Encalypta ciliata* is known from the Black Hills in South Dakota and Wyoming, from one locality in northern Nebraska and one in northeastern Iowa. In the Great Lakes region, *E. ciliata* has a more-or-less continuous distribution eastward to the coast from western Ontario, through southern Ontario, northeastern Minnesota, northern Michigan, southern Quebec, Vermont, northern Maine, and New Brunswick to Nova Scotia, Prince Edward Island and Newfoundland. There are only a few sporadic records from the Hudson's Bay area, but it probably is not infrequent in northern Ontario and Quebec (Fig. 192). *Encalypta ciliata* has been reported from a number of coastal localities in southern and central Greenland (Lewinsky & Mogensen (1977) - indicated on the map by open circles because the specimens requested from C have not been available to me). In South America, *E. ciliata* has been collected sporadically along the Cordilleran axis in Colombia, Peru, Bolivia and Patagonia. The disjunctions probably represent, for the most part, disjunct collecting localities.

Variation: (1) In general, the superficial structure of spores is one of the most reliable means for differentiating species of *Encalypta*. Spores of a number of different species, including *E. ciliata*, have recently been illustrated with SEM's by Vitt and Hamilton (1974) and Járai-Komlódi and Orbán (1975). In both studies, spores of *E. ciliata* were reported to be distinctly polar with a central trilete mark and numerous, radial ridges on the proximal face, and the distal face differentiated by five or six radial ridges and a central brochus (or bordered pit). Vitt and Hamilton also noted that the surface of the spore is generally smooth or pitted, but that small papillae are occasionally present. Járai-Komlódi and Orbán considered the structure of spores of *E. ciliata* to be so distinctive that they placed it in a group separate from all other species of *Encalypta*, as noted in the Introduction. While Vitt and Hamilton grouped *E. ciliata* with several other species of *Encalypta*, they similarly considered the features described above to be of great value in identification. However, the results of an extensive light microscope investigation of spores of *E. ciliata*, indicate that there is considerable inter-populational variation in the

Figure 192. Distribution of *Encalypta ciliata* in North America.


NORTH AMERICA
No. 2
SCALE
MILES
KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
120
110
100
90
80
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR
Prepared by Henry M. Leppard

structure of the distal surface (Figs. 194-199, 205-210). The distinctive brochus and radial plicae or ridges (Figs. 194-195) described and illustrated in the two papers cited above are, in many populations, indistinct (Figs. 195, 209) or so obscured by other structural features (Figs. 199, 205, 207) as to be virtually invisible when observed with the light microscope. Indeed, the variation that occurs in the structure of the distal surface is such that there are no features that can be considered reliable for differentiating E. ciliata. In contrast, the structure of the proximal surface is remarkably stable in different populations. The triradiate mark and the numerous radial plicae are always visible with the light microscope, although there may be some irregularities around the trilete mark (Figs. 200-204). While it is not always visible with the light microscope, another definitive feature of E. ciliata is that the entire surface of the spore is always more-or-less distinctly pitted (Figs. 193-210).

(2) For the most part, the Northern Hemisphere populations of E. ciliata are remarkably uniform in character-states of the calyptra, capsule, peristome and leaves, as described above under Diagnosis and Differentiation. In contrast, a more-or-less marked plasticity in the states of these same characters differentiates Southern Hemisphere and Mexican populations of E. ciliata. In addition, a few isolated populations are each characterized by highly divergent states of one or a few characters. Probably coincidentally, each of these latter populations shares the common feature of a more-or-less papillose calyptra. A discussion of the characteristics of these "atypical" populations of E. ciliata follows and the taxonomic implications are assessed.

(a) Mexican and South American Populations. Populations of E. ciliata from Mexico southward through Central and South America are discussed as a unit as the patterns of variation that occur are very similar. In some populations, the calyptrae are virtually indistinguishable from those that typify the more northerly populations. The rostrum is long, relative to the cylinder length (approximately two-thirds the length of the cylinder), well-defined and narrow, by comparison to the breadth of the cylinder from which it is quite distinctly contracted, and the ridge at the base of the cylinder is very distinct with a long, regularly segmented fringe hanging pendent from it (Fig. 212 - lower centre). However, the relative length of the rostrum is variable and in some populations it is considerably less than two-thirds the length of the cylinder (for example, it is not even

Figures 193-198. *Encalypta ciliata*. Variation in Spores.

Fig. 193. Triad. Scale=20 µm.

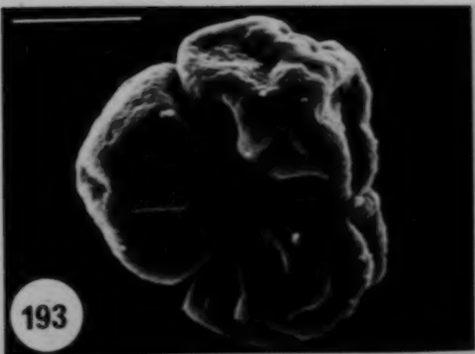
Figs. 194-198. Distal surface.

Figs. 194-195. Scale=10 µm.

Fig. 196. Scale=4 µm.

Fig. 197. Scale=10 µm.

Fig. 198. Scale=2 µm.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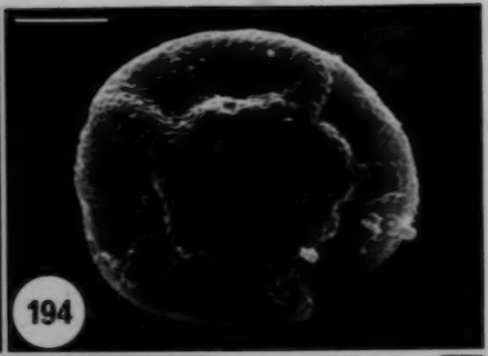
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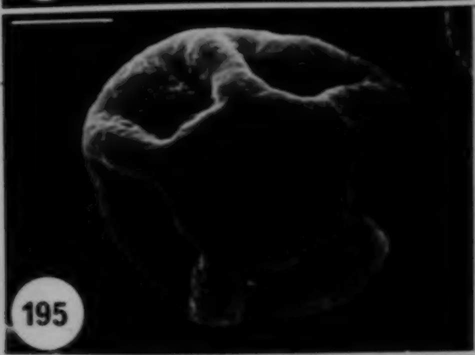
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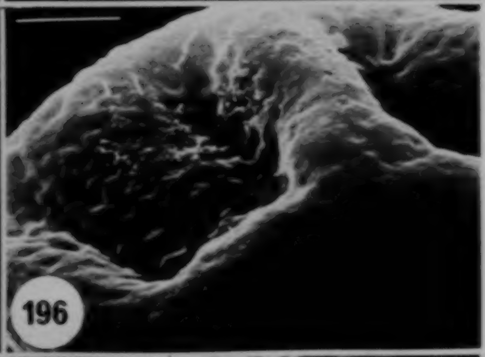
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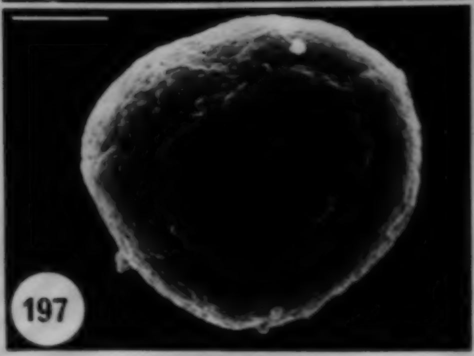
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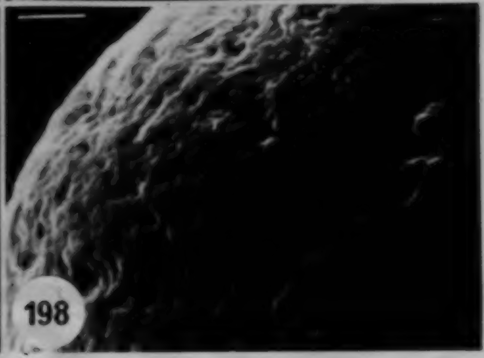
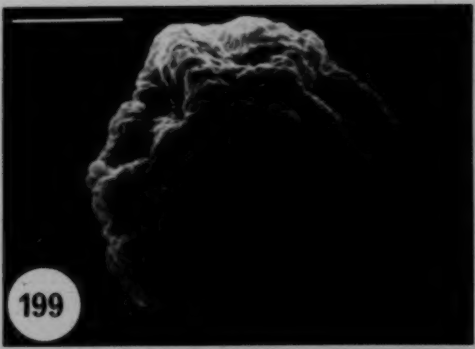

198

Figures 199-204. Variation in Spores (cont'd.)

Fig. 199. Distal surface. Scale=10 μm.

Figs. 200-204. Proximal surface.

- Figs. 200-201. Scale=10 μm.
- Fig. 202. Scale=2 μm.
- Figs. 203-204. Scale=10 μm.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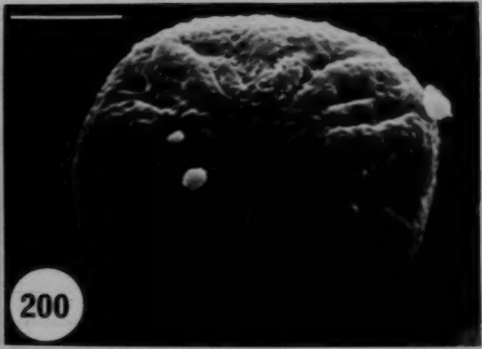
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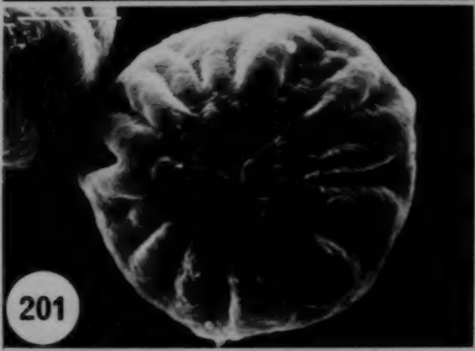
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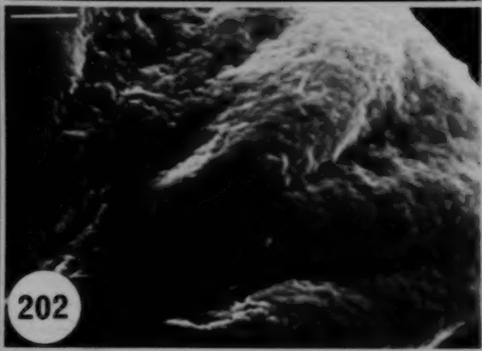
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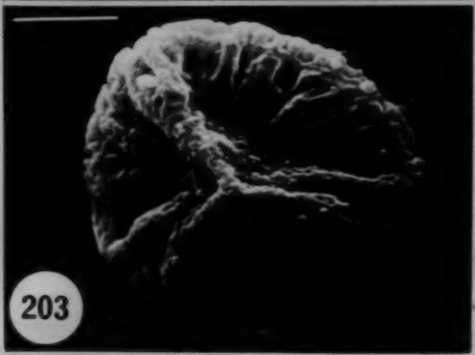
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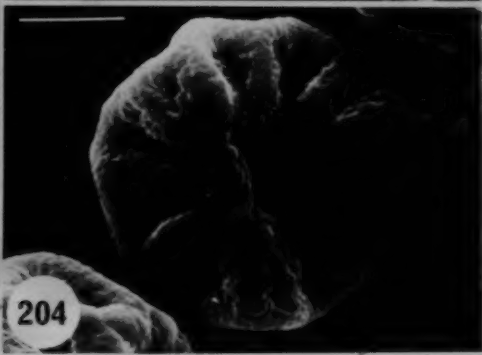

204

Figures 205-210. **Encalypta ciliata**. **Variation in Spores** (cont'd.). Distal Surface.

Fig. 205. Scale=10 μm.

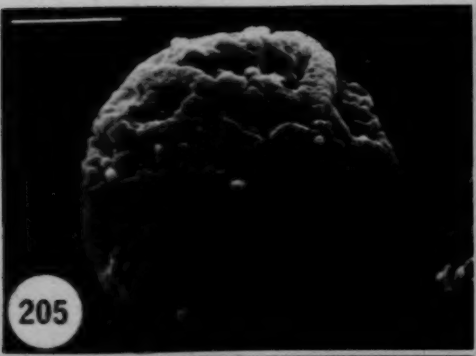
Fig. 206. Scale=5 μm.

Fig. 207. Scale=10 μm.

Fig. 208. Scale=2 μm.

Fig. 209. Scale=10 μm.

Fig. 210. Scale=2 μm.



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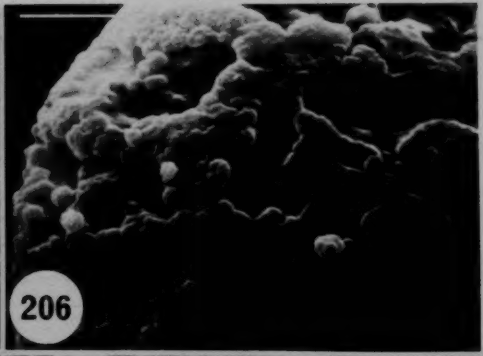

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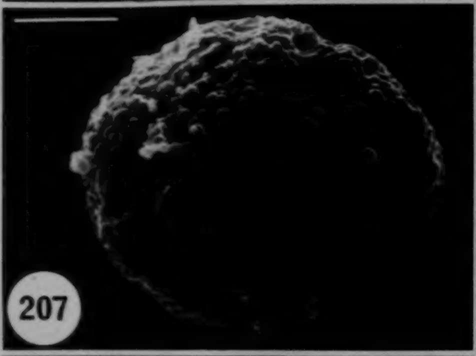

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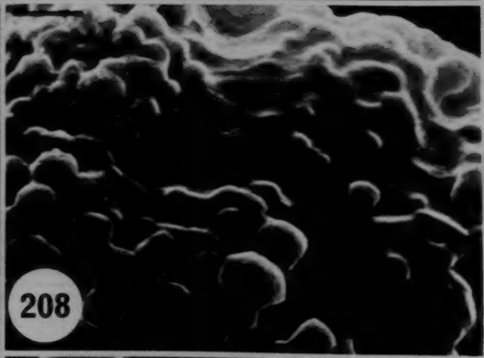

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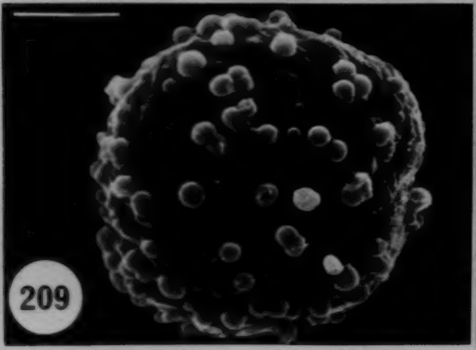

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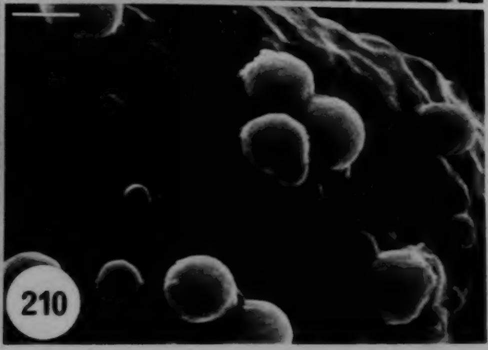


210

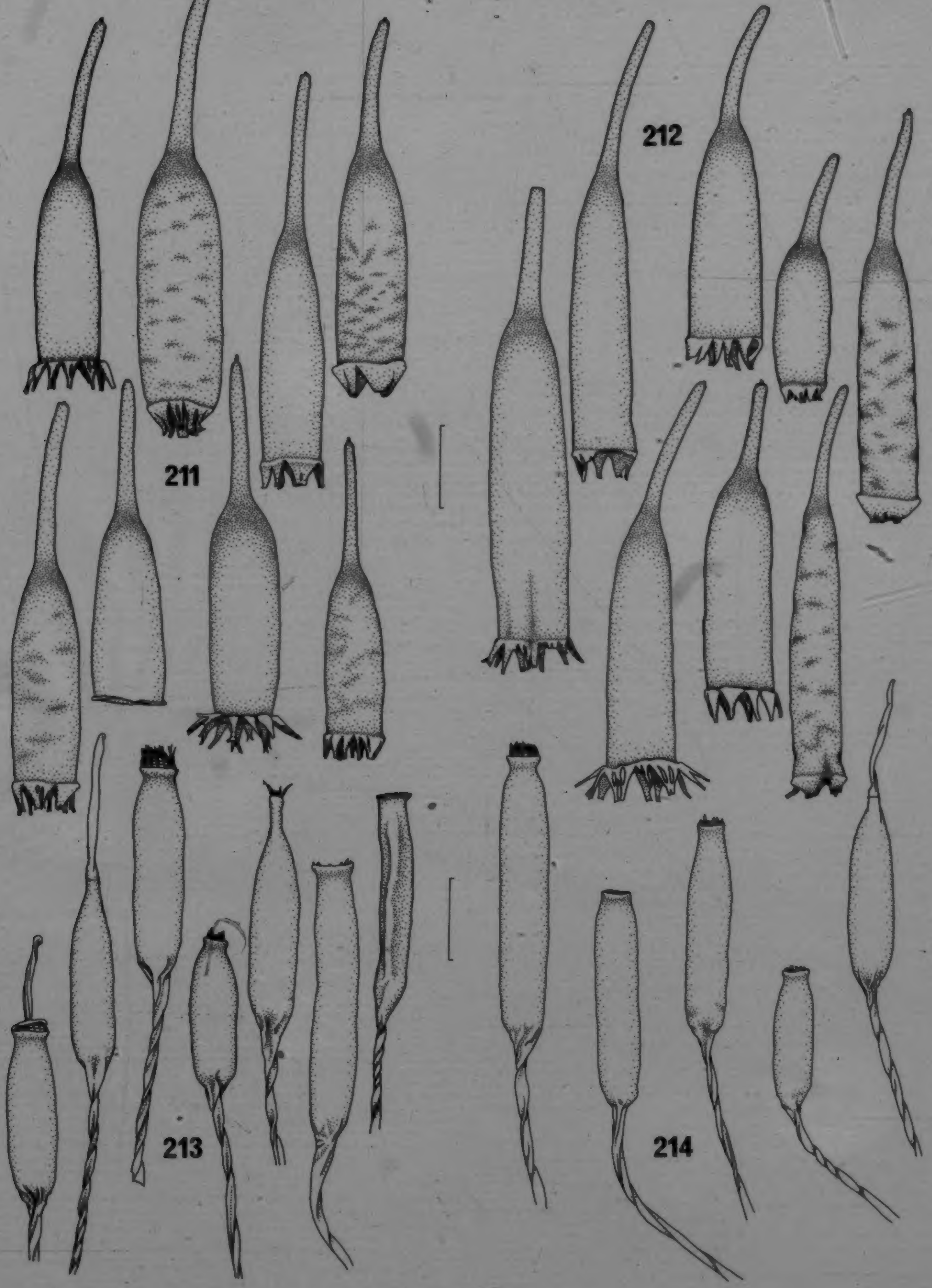
Figures 211-214. **Encalypta** **ciliata**. Scale=1 mm.

Fig. 211. Calyptrae of "Typical" Northern Hemisphere Populations.

Fig. 212. Calyptrae Showing Variation in Southern Hemisphere and Mexican Populations.

Fig. 213. Capsules of "Typical" Northern Hemisphere Populations.

Fig. 214. Capsules Showing Variation in Southern Hemisphere and Mexican Populations.

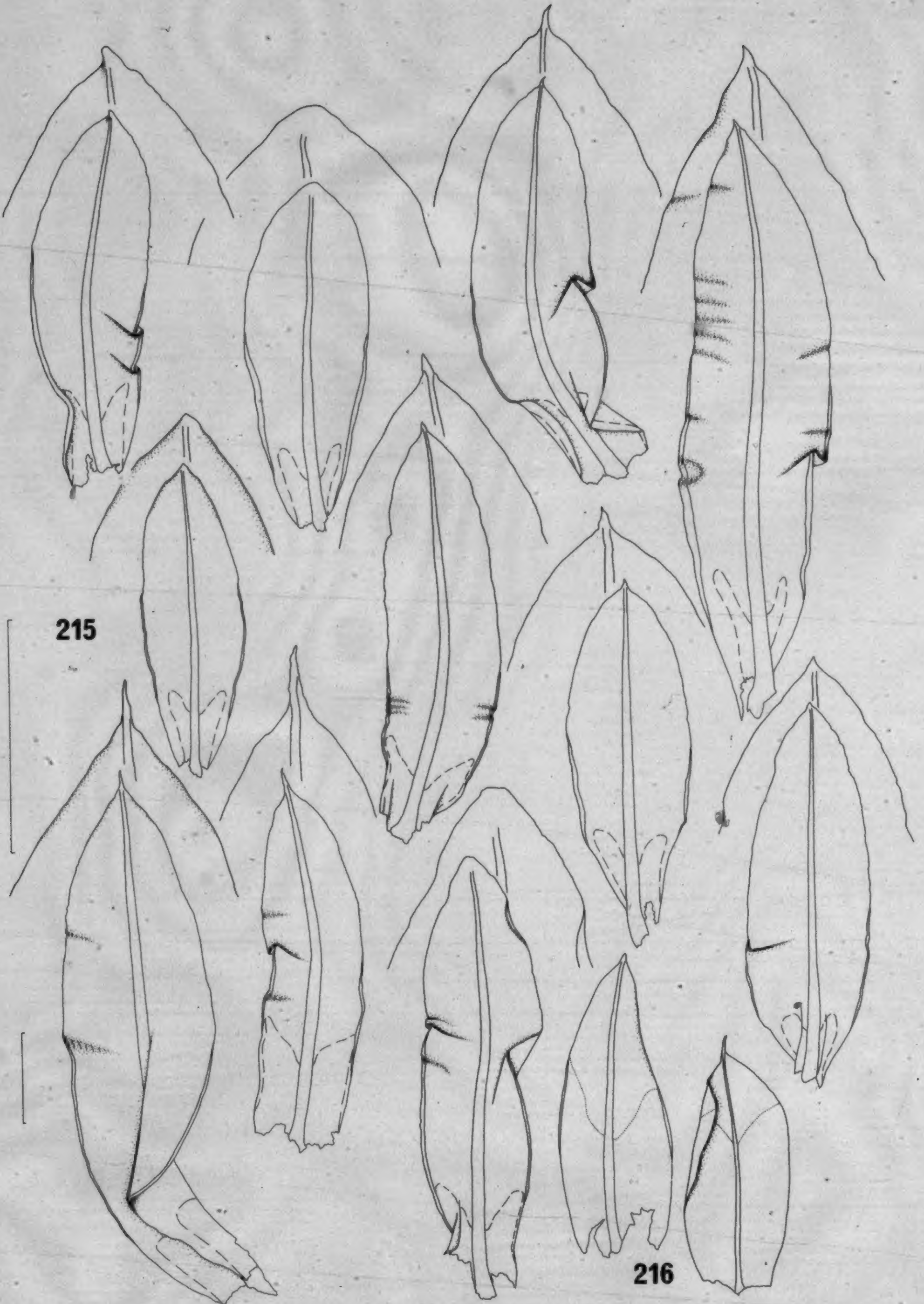


one-half the length in Fig. 212 - left). The diameter of the cylinder is atypically narrow in some populations, and then the rostrum appears less distinctly contracted (Fig. 212 - lower right). In some, the ridge at the base of the cylinder is poorly defined and more-or-less oblique rather than horizontal (Fig. 212 - lower right, upper left). Similarly, there is considerable variability in the coloration of the calyptra. Typical of *E. ciliata* are populations with the calyptra pale-golden and transluscent throughout. However, in many the fringe is pale-brownish, which also occurs in sporadic Northern Hemisphere populations, but in some South American populations it is very dark-brown. Such coloration does not characterize any of the northerly populations. Also, the entire calyptra is quite opaque and brown in some; golden with rusty-colored streaks on the rostrum and the upper part of the cylinder in others. There is also considerable variation in capsule shape and development of the peristome. Capsules of some collections are cylindric with a distinct constriction just below the mouth (Fig. 214 - left), as is characteristic of *E. ciliata*, but in others this constriction is poorly defined or even lacking, and the mouth is quite small (Fig. 214 - centre, 232). Some have a peristome that is well-developed with dark-orange teeth, which exemplifies *E. ciliata*; however, in other instances the teeth are sparse, fragile and transluscent (Figs. 51, 64, 214 - centre, centre-right), and in others still, they are never formed (Fig. 214 - left centre). The setae are very short in some populations, but this is also a feature of some Northern Hemisphere populations, particularly those growing in tundra habitats. Shape of the leaf apex and, to some extend, recurvature of the leaf margins are subject to variability (Figs. 215-216). Some plants have leaves with a mucronate apex, as in typical *E. ciliata*, but others are muticous with the costa ending well below the apex, which tends to be cucullate, and some are apiculate with the point somewhat more elongated than is usual. Also, the margins are strongly, but narrowly recurved in most populations, which is characteristic of *E. ciliata*. However, there are sporadic populations with the margins so finely recurved that it is virtually impossible to detect with the dissecting microscope or, at the other extreme, they are relatively broadly recurved. The variation described above is expressed, primarily, between different populations; however, there is also limited intrapopulational variability. For example, within a single population, the development of the peristome varies from absent to rather well-developed with 16, orange teeth.

Figures 215-216. Encalypta ciliata - Variation in Leaves of Southern Hemisphere and Mexican Populations. Scale=1 mm.

Fig. 215. Vegetative leaves.

Fig. 216. Perichaetial leaves.



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Similarly, the leaves are muticous on some plants and mucronate on others.

The populations of *E. ciliata* that exhibit this marked phenotypic plasticity in taxonomically critical character-states are quite clearly delimited geographically by their occurrence in the New World from Mexico southward. However, within this broad geographic area, these populations appear to be independently distributed. For example, populations that are more-or-less typical of *E. ciliata* occur in scattered localities in Mexico, and southward in Guatemala, Colombia, Peru and Patagonia. In fact, one of the types of *E. austrociliata* from Patagonia has some more-or-less "aberrant" capsules, which is quite a common feature of the Northern Hemisphere populations of *E. ciliata* (see Diagnosis and Differentiation of *E. microstoma*). Similarly, populations with features atypical for *E. ciliata* are sporadically distributed. This is particularly true of Mexico, where virtually the entire range of variation described above is exhibited by different populations in the relatively small area encompassed in the central and northern portions of that country. Therefore, there is no indication of clinal modification of particular character-states correlated with geographic occurrence.

Just as there is only a broad correlation between the atypical populations of *E. ciliata* and their distribution, there are only vague indications that the modification of one character-state is correlated with that of another. For example, among the Mexican populations of *E. ciliata*, there is a tendency for plants with a very fragile peristome or peristome absent to have a short seta and muticous leaves with the margins imperceptibly recurved, but these character-states generally are not all correlated within individual populations. The type of *E. mexicana* consists of plants with a short seta and fragile peristome, but the leaves are mucronate and distinctly revolute, as is typical for *E. ciliata*. The tendency for these three character-states of peristome, seta and leaves to be correlated is expressed also in some South American populations; however, quite different combinations of character-states also occur. For example, the holotype of *E. coarctata* has a very fragile, poorly-developed peristome, but the leaves have a particularly strong, prominent mucro (more pronounced than is typical for *E. ciliata*). *Encalypta leiotheca* was described from a Bolivian collection the capsules of which lack a peristome, but the setae are moderately long and quite within the range characteristic of *E. ciliata*. Most of the Mexican populations are characterized by a pale-brown calyptra fringe whereas very dark-brown fringes have been observed only in some South American collections. Variation in calyptra structure and color seems quite independent of variation in other character-states. In some Mexican populations, the calyptrae are quite atypically elongate and narrow in the cylinder, yet in all other respects the plants are indistinguishable from those typical of E. ciliata. On the other hand, some populations that are typical in other character-states, for example, peristome absent, seta short and leaves muticous, have calyptrae that are characteristic of E. ciliata.

Studies of populational and regional variation in bryophytes are limited, as reported by Vitt (1980b), but are an essential basis for taxonomic evaluations (Vitt 1980b, Zander 1978). Zander (1978) stated "...that only study of intraspecific variation of a species and of related species on a worldwide basis can provide a sense of proportion that allows the kind of taxonomic appraisal that satisfactorily reflects evolutionary and migratory history.". Encalypta ciliata is a case in point. After I had studied many populations of E. ciliata from throughout its range in the Northern Hemisphere (excluding Mexico), I had the feeling that here is a very clearly-defined, distinct species that posed no taxonomic problems. When I encountered one of these atypical New World specimens for the first time, my immediate reaction was that this was something quite different from E. ciliata, perhaps distinct at the specific or at least some subspecific level. It is not surprising that when Mitten examined such a population, he described E. coarctata (Mitten 1869) or that Herzog (1916) described E. leiotheca. Recently, Zander (1977, 1978 and 1979) has brought to our attention that numerous nomenclatural designations for pottiaceous taxa similarly reflect "...extreme expressions, permutations of character states, and geographic variants..." (Zander 1979). However, both Zander (1977, 1979) and Vitt (1976, 1980b) have recognized that regional intraspecific differentiation occurs in some moss species, whether or not the differences are given nomenclatural recognition. Also, Zander (1977, 1978) has reported that a number of taxa are characterized by gradients in structural variation, for example Bryoerythrophyllum jamesonii (Tayl.) Crum. However, my studies of the populations of E. ciliata from Mexico, Central and South America indicate that there is no combination of character-states, nor even one constant character-state that differentiates these populations. It can only be stated that they are characterized by a greater range of phenotypic expression, possibly reflecting greater flexibility of the genotype and/or lengthy isolation from the North American (excluding Mexico) populations. This is precisely the same situation that Zander (1977) described for the West Indian populations of Hymenostylium recurvirostrum (Hedw.) Dix. He reported that these are characterized by "...a great variety of character state combinations and in aggregate differ significantly from continental collections in the greater frequency of unusual combinations of character states.". Zander concluded that "No satisfactory circumscription of a West Indian taxonomic entity can be made..." and "recognition of all permutations of character state combinations would lead to a multiplicity of artificial taxa.". Similarly, I have concluded that the populations of E. ciliata from Mexico, Central and South America cannot be distinguished taxonomically and should not be given nomenclatural recognition; they represent variation that is inherent in at least some populations of E. ciliata.

(b) African Populations. In general, the African populations are considerably less variable in their structure than those described above from Mexico-South America. In part, this may reflect the fact that considerably fewer collections representing only a few localities are known from Africa. However, even considering this, the African populations show less divergence from the typical Northern Hemisphere populations. The calyptrae are typical for E. ciliata in every feature, as is the length of the seta. Similarly, capsule shape is quite characteristic, but these populations do differ in the development of the peristome. In general, most of the African populations of E. ciliata are characterized by a poorly-developed, fragile peristome. The leaves are as the Northern Hemisphere ones, except for one population from Lesotho (Jacot-Guillarmod 6081 - MO) with muticous leaves (Fig.). Another collection from this same area has typically mucronate leaves (Magill 4412 - ALTA). As with the Mexican-South American populations, these ones from Africa are geographically isolated. However, the development of the peristome is variable and there seems little basis for taxonomic recognition of these populations as distinct from E. ciliata at any level.

There are several collections of E. ciliata s. lat. from Ethiopia that are puzzling and do not fit the pattern of variation described above. These were collected between 1837 and 1842 by Wilhelm Philipp Schimper's cousin, Wilhelm Schimper, who was hired to collect plants in various rather inaccessible regions (cf. Sayre 1969). Schimper's

Abyssinian collections were published as *Schimperi Iter Abyssinicum* and distributed by Unio Itineraria (the group of botanists who hired Schimper to collect for them) (Sayre 1969). One of these collections, No. 492b, was labelled with the *nom. nud.* of *E. cuspidata* Bruch *et* Schimper and two others (Nos. 430 and 470) were published as *E. ciliata* var. *gymnostoma* Bruch *et* Schimper, also a *nom. nud.* In all three instances, the authority names were followed by "(Bryol. europ.)"; however, these names were never published in Bryologia Europaea. Later, Carl Müller described *E. cuspidata* Bruch *et* Schimp. *ex* C. Müll. and cited the Schimper exsiccata specimen of 492b. After assessing the duplicates of this specimen in various herbaria, it appears to have consisted of a mixture of *E. ciliata* with a poorly developed peristome, as is found in many African populations and described above, and a form of *E. rhaptocarpa* with gymnostomous capsules, short setae, leaves with a prominent costa and long hair-points. Müller's description appears to have included both these taxa. In addition, he emphasized the purple coloration of the plants, which clearly is a reference to a third taxon, probably a species of Bryaceae, which is also intermixed. Müller apparently did not have a clear concept of what he was describing, but it is possible to select a type that more-or-less accords with the original description. There is a specimen in BM with "E. cuspidata nob." written on it in Schimper's handwriting. Although Un. It. 592 is the number indicated on this collection, I feel reasonably certain that this must have been a part of No. 492b (Sayre (1969) suggested that there were probably only Nos. 400 to 500 in Schimper's exsiccata from Abyssinia). Because this specimen is in Schimper's herbarium and Müller attributed *E. cuspidata* to Bruch and Schimper, it seems appropriate to lectotypify a specimen that Schimper considered to be this species as Müller's herbarium has been destroyed. Therefore, this specimen, which consists only of the form of *E. rhaptocarpa*, has been lectotypified.

Specimen 470 appears to have been a mixture of more-or-less "typical" *E. ciliata* (as described above) and a quite different form of *E. ciliata*. Specimen 430 consists entirely of this latter form of *E. ciliata*. Also, there are other specimens of this form in Schimper's herbarium with the manuscript names of *E. rufociliata* and *E. rufofimbriata*. It is difficult to assess the taxonomic status of this taxon at the present time. The plants are superficially sharply differentiated from other African and Eurasian populations by gymnstomous capsules that are quite inflated at the base and then narrowed to a smaller mouth, short setae, and smoky-colored, opaque calyptrae with a short rostrum. It is possible that some of these plants for at least one of the collections (for example, number 470) were growing intermixed with plants of *E. ciliata* that are quite characteristic of the variation found elsewhere in Africa for this species. This would lend considerable weight to an argument that these populations represent a distinct, presently undescribed taxon. However, I feel that it is quite possible and perhaps probable that Schimper did not find these potentially different taxa growing intermixed; in all of the exsiccata specimens that I have seen, they are each in different patches on the sheet. Also, while these plants appear sharply differentiated structurally from the other African populations, they are really no more different than some of the Mexican and South American populations when these are viewed in isolation. Therefore, at the present time, I feel that it is prudent not to give these African populations taxonomic recognition until more specimens from this region are available for comparative purposes.

(c) *Encalypta scabrata*. When Bartram (1933) described *E. scabrata* from the Island of Maui in Hawaii, he stated that it differed from *E. ciliata* "...principally in the very scabrous calyptra but also in the longer leaf apiculus.". Indeed, many of the Hawaiian populations are characterized by these features (Fig.); however, some have the calyptra virtually smooth throughout and the apiculus no longer than is typical for *E. ciliata* (Fig.). Therefore, *E. scabrata* is considered to be taxonomically synonymous with *E. ciliata*. Similarly, Vitt (1980b) found that the Hawaiian populations of *Macrocoma tenue* (Hook. *et* Grev.) Vitt subsp. *sullivantii* (C. Müll.) Vitt are somewhat differentiated, but are not discontinuous from other populations of this species because of the occurrence of intermediates.

It is interesting to note that in the type specimens of *E. scabrata* many of the plants have more-or-less "aberrant" capsules (see Diagnosis and Differentiation of *E. microstoma*), although no reference was made to these in the original description. The occurrence of such "aberrant" capsules is further evidence of continuity between the Hawaiian populations of *E. ciliata* and those found in other widespread geographic regions.

Phylogenetic Relationships: The two species that are most closely related to *E. ciliata* are *E. sibirica* and *E. microstoma*; for a discussion, see Diagnosis and Differentiation of each of the latter species. There are also a number of characteristics that link *E. ciliata* with *E. brevipes* and *E. brevicolla*. These are enumerated under Phylogenetic Relationships of each of these species.

Specimens Examined: ALTA (200), BISH (6), BM (45), BP (7), CANM (280), CM (1), DUIS (12), F (85), FH (7), FLAS (3), Priv. Herb. J.-P. Frahm (6), G (3), H (100), H-Br (75), H-Sol (45), Priv. Herb. P. & E. Hegewald (2), Priv. Herb. W. J. Hoe (7), Priv. Herb. D. G. Horton (75), HSC (14), IRK (45), JE (3), KRAM (8), L (95), M (255), MEXU (13), MIN (5), MO (130), NFLD (16), NY (305), PC (11), S (180), TENN (18), UBC (155), UWSP (7), W (2), WIS (1), Priv. Herb. B. van Zanten (1).

ENCALYPTA SIBIRICA (Weinm.) Warnst.,

Hedwigia 53: 316. 1913.

Basionym: *Encalypta ciliata* Hedw. var. *sibirica* Weinm., Bull. Soc. Natural. Moscou 18(2): 448. 1845. Type: "In Sibiria prope Irkutsk. Aestate. (Vidi in herb. Acad. Scien. Petrop.)." (Lectotype: "Sibiria, Irkutsk ex hb. sc. petropol." H-Br!).

Encalypta laciniata (Hedw. *ex* Lindb.) Lindb. subsp. *sibirica* (Weinm.) Lindb., Act. Soc. Sci. Fenn. 10: 268. 1873.

Leersia laciniata Hedw. *ex* Lindb. subsp. *sibirica* (Weinm.) Lindb. *et* H. Arnell, Kongl. Svenska Vetenskapsakad. Handl. 23(10): 64. 1890.

Leersia sibirica Lindb. *et* H. Arnell *ex* Par., Ind. Bryol. ed. 2, 2: 121. 1904.

Nomenclatural Notes: According to Sayre (1977), Weinmann's herbarium is possibly located in LE, but I have never received any response to my requests for a loan of their specimens of Encalyptaceae. Therefore, I feel that I have no alternative but to select a lectotype of *E. sibirica* elsewhere, if possible. Unfortunately, the one type of *E. sibirica* that I have seen is a sparse and rather battered specimen in H-BR, but it is identifiable and is here designated the lectotype.

Discussion: The lectotype of *E. sibirica* is in such poor condition that critical taxonomic features have been obliterated in some of the plants. Previously, when I examined this specimen, I had been able to determine, in agreement with Lindberg (1873), that it is differentiated from *E. ciliata s. str.* by a papillose calyptra and the lack of a peristome. However, in view of the variation that is known to occur in *E. ciliata* in some regions of the world (see discussion of Variation in *E. ciliata*), I hesitated to give this entity any taxonomic recognition, particularly on the basis of a single, less than adequate specimen. Therefore, I considered *E. sibirica* to be synonymous with *E. ciliata*.

Recently (June 1981), I received a loan of specimens of *Encalypta* from PE. Among them was one (*Y.-C. Cheu* VI-VII. 1934) containing plants of a taxon that I recalled having seen only once before in a specimen from Ulaanbaatar in Mongolia (*Schubert* 27.7.1968 - MO). As with the specimen of *E. sibirica*, I had been uncertain of how to treat the Mongolian specimen taxonomically. It too is clearly very closely related to *E. ciliata*, but the plants are characterized by a densely papillose, opaque calyptra and the rostrum is indistinctly defined as is the poorly defined oblique extension at the base of the cylinder. Also, the fringe is pale-brown and the cells of the fringe are more broadly oblong than is typical for *E. ciliata*. The capsules are immature, but appear to have no peristome and the leaves are hair-pointed. I suspected that this taxon is distinct, possibly at the specific level, but the immature capsules (the spores are still enclosed in the spore mother cells and the superficial structure of the exospore is indistinct) and the knowledge of the variability inherent in some populations of *E. ciliata* made me feel that I should wait to see more material before making any taxonomic decision.

The PE specimen is characterized by the same features as those described above for the Mongolian specimen. Furthermore, the former specimen has plants with capsules that are very close to being completely mature. There is definitely no trace of a peristome and the spores are characterized by a rugulate pattern of vermiform protuberances on the distal surface. The discovery of a second specimen similarly differentiated from *E. ciliata* and from the same general geographic area (the specimen from PE is from Hopeh province in the vicinity of Peking) motivated me to re-examine the type of E. sibirica, which was collected at Irkutsk. I discovered that some of the plants in the latter specimen have hair-pointed leaves, but that many of the hair-points have been broken off, which misled me originally. Also, the structure of the distal surface of the spores is the same as that described above. Therefore, I have concluded that E. sibirica is a distinct species with the characteristics noted above; in all other respects it is more-or-less like E. ciliata.

The discovery of a connection between the three Asian specimens, and the analysis of the definitive features of E. sibirica brought one further specimen to mind. This specimen, from southwestern Texas (Magill 195 - MO), is characterized by some character-states that are markedly divergent from those typical for E. ciliata. Again, because there was a single specimen I previously felt it best to consider it within the broad concept of E. ciliata. However, a reassessment of the plants leads me to believe that this is a specimen of E. sibirica s. lat. The plants of the specimen from Texas are different from those of E. sibirica in only one feature, that is , the leaves are muticous. While this may represent a taxon distinct from E. sibirica, I would prefer to wait until I have seen more Asian and, hopefully, North American material of E. sibirica before making a decision on the taxonomic status of this taxon.

It may be that E. sibirica is extremely rare, even within its range. Although the type collection is from Irkutsk, there is not one specimen of E. sibirica among the 44 of E. ciliata in IRK.

While some of the Hawaiian populations of E. ciliata parallel E. sibirica in the characteristic of a papillose calyptra, the structure of the papillae is different. In E. sibirica, the papillae are dense and more-or-less branched, while those in the Hawaiian populations of E. ciliata are relatively sparse, low and rounded. Some of the Hawaiian populations of E. ciliata with papillose calyptrae are also characterized by apiculate leaves in contrast to the short mucro that defines most populations of E. ciliata. However, this apiculus is stout and brown; therefore, it is quite different from the flexuose, hyaline hair-point that defines E. sibirica.

A full description and illustrations of E. sibirica will be published in the future when I have access to more specimens.

ENCALYPTA MICROSTOMA Balsamo et De Notaris,

Mem. Reale Accad. Sci. Torino 40: 342. 1838.
Figs. 12, 14, 29, 32, 36, 217–237.

Type: "In monte Adula, BRAMBILLA." (Holotype: "Encalypta microstoma DNtrs in monte Adula leg. Brambilla 1836. ex Prof. Balsamo." RO–De Notaris!; Possible Isotype: "fr. Gottardo Encalypta microstoma DNtrs Bals." BM–Hampe!).

Encalypta ciliata Hedw. var. *microstoma* (Bals. *et* De Not.) Husn., Musc. Gall. 198. 1888. *Hom. illeg.* of *E. ciliata* var. *microstoma* Schimp.

Encalypta laciniata Hedw. *ex* Lindb. var. *microstoma* (Bals. *et* De Not.) Broth., Act. Soc. Sc. Fenn. 19(12): 37. 1892.

Encalypta ciliata Hedw. subsp. *microstoma* (Bals. *et* De Not.) Kindb., Eur. N. Am. Bryin. 2: 297. 1897.

Leersia laciniata Hedw. *ex* Lindb. var. *microstoma* (Bals. *et* De Not.) Möller, Bot. Not. 1907: 142. 1907.

Nomenclatural Notes: *Encalypta microstoma* was described in 1838 (Balsamo & De Notaris 1838). At the varietal level, the epithet *microstoma* was first described by Schimper in the Corollarium (1855) as *E. ciliata* var. *microstoma*. Therefore, all later authors, except Husnot (1888), apparently assumed that Schimper's variety *microstoma* was a new combination based upon Balsamo and De Notaris' *E. microstoma*. While there is no specimen of *E. ciliata* var. *microstoma* in Schimper's herbarium, details of the original description provide reasonably good evidence that Schimper was not referring to *E. microstoma*. His description is of a structural modification of capsules of *E. ciliata*. Taxonomic confusion has arisen because of the striking resemblance between capsules of *E. microstoma* and some of these "aberrant" capsules of *E. ciliata*, and nomenclatural confusion has been created by Schimper's presumably coincidental use of the epithet *microstoma*. Therefore, *E. ciliata* var. *microstoma* Schimp. is considered to be synonymous with *E. ciliata*, not with *E. microstoma*. See Diagnosis and Differentiation (below), and Horton (1981b) for further details.

Diagnosis and Differentiation: Encalypta microstoma is characterized by a smooth, golden-brown calyptra with a relatively broad, slightly curved or erect rostrum and a dark-brown, glisteny, well-defined fringe, which hangs more-or-less pendent from a narrow, horizontal or slightly oblique expansion at the base of the cylinder. The gymnostomous capsules (a fragmentary, rudimentary peristome has been observed in very few populations) are narrowly cylindric to cylindric, tapered slightly distally and more-or-less contracted in the upper part to the small mouth, and gradually narrowed to the seta. Yellow to copper tones characterize the capsule and seta. Leaves are muticous with plane margins and a prominent costa, which ends just below the apex, except in the perichaetial leaves (in these it is percurrent). Microscopically, the transverse section of the capsule wall is distinctive. The radial-longitudinal and outer tangential walls of the exothecial cells are very strongly thickened giving the appearance of a cut-out paper chain of tulips; in superficial view these thickenings almost obscure all but a narrow, central strip of the cell lumina. In the lower part of the leaf there is a well-defined marginal border of pale green cells that contrasts with the laminal cells, which are defined by dark-orange transverse walls. The papillae on the abaxial surface of the transitional cells extend to the basal cells and the abaxial surface of the costa is more-or-less smooth. In transverse section there are two to three rows of stereids in the costa. The spores are heteropolar with a more-or-less distinct trilete mark and numerous, radial plicae on the proximal surface. The distal surface is more variable with a more-or-less distinct central pit bordered by a thick, more-or-less prominent rim connected to five to seven more-or-less prominent plicae. In some instances, the pit, rim and plicae are overlain by anastomosing verrucae, which give a reticulate impression under the light microscope. Both surfaces are more-or-less distinctly, minutely pitted.

The striking structural similarity between E. microstoma and E. ciliata leaves no doubt as to the phylogenetic derivation of the former taxon. Indeed, these two species are but narrowly differentiated from one another; however, there are a number of character-states in which the two taxa are consistently different. Encalypta microstoma can be differentiated from E. ciliata by the darker color of the calyptra, including the fringe, which is a rich brown; calyptrae of E. ciliata are generally pale-golden throughout, although the fringe may be pale-brown in some populations. Also, the shape of the

Figures 217-221. Encalypta microstoma. Scale=1 mm.

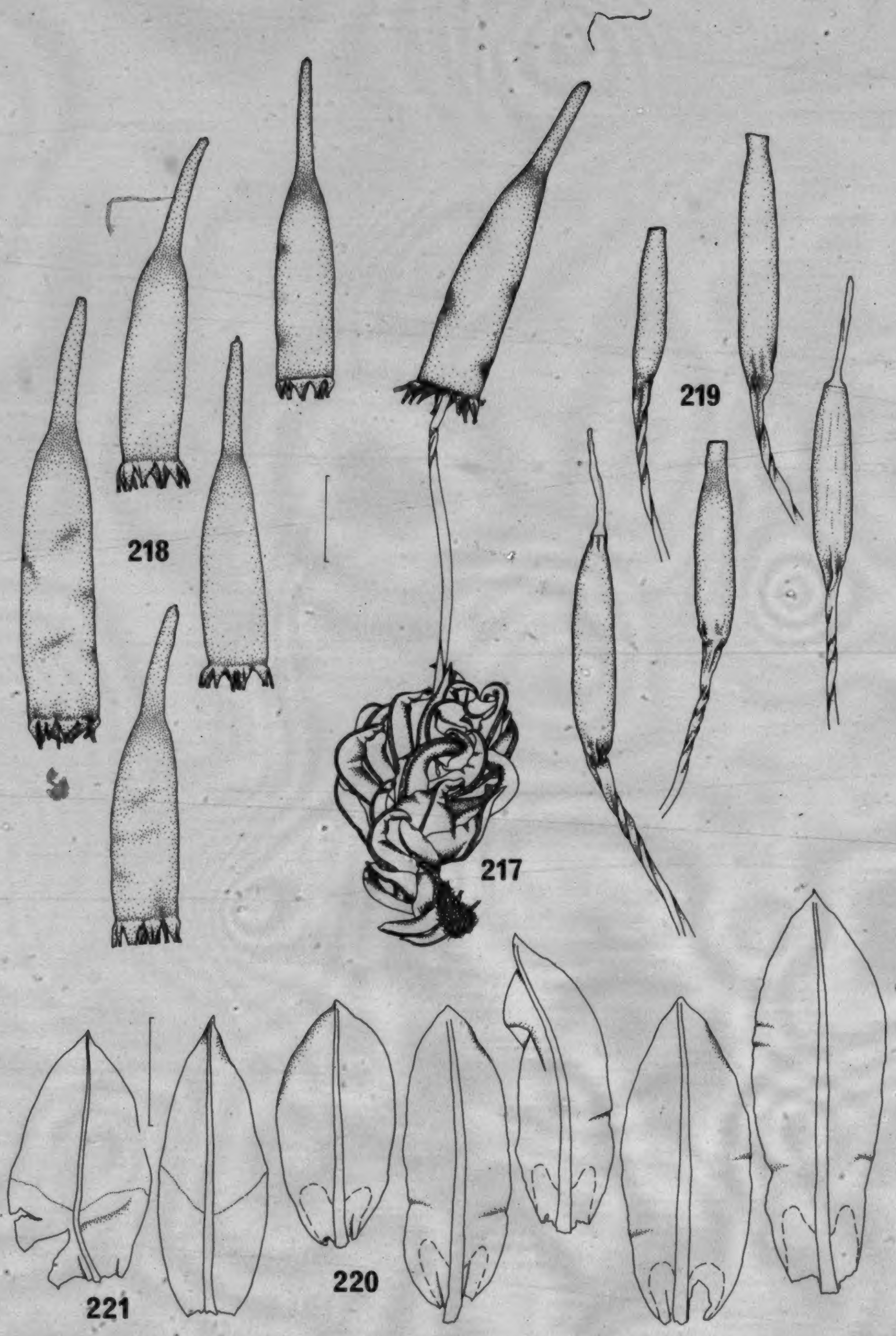
Fig. 217. Habit.

Fig. 218. Calyptrae.

Fig. 219. Capsules.

Fig. 220. Vegetative leaves.

Fig. 221. Perichaetial leaves.



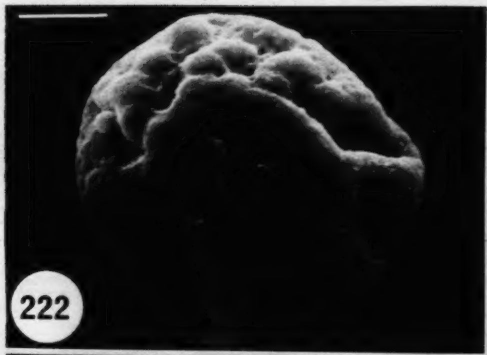
Figures 222-227. *Encalypta microstoma*. Variation in Spores. Distal Surface.

Fig. 222. Scale=10 μm.

Fig. 223. Scale=4 μm.

Figs. 224-226. Scale=10 μm.

Fig. 227. Scale=4 μm.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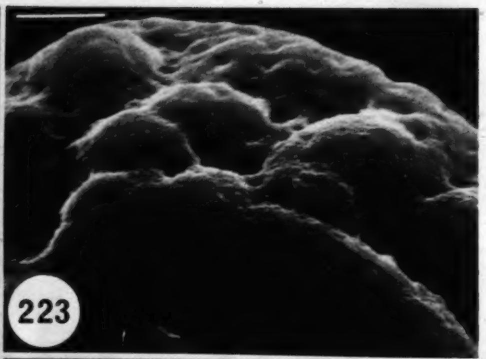
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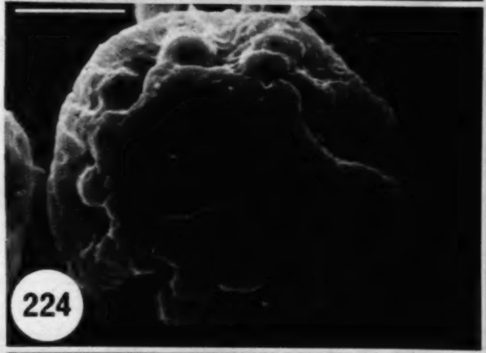
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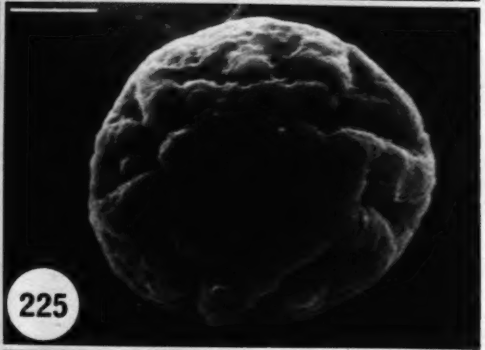
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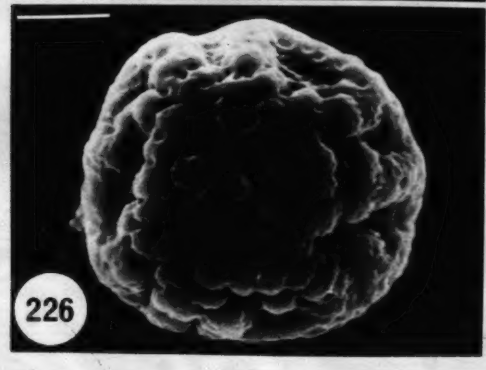
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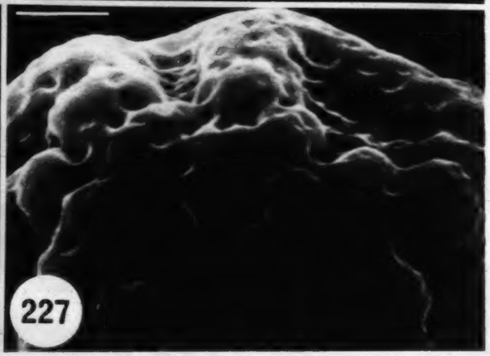
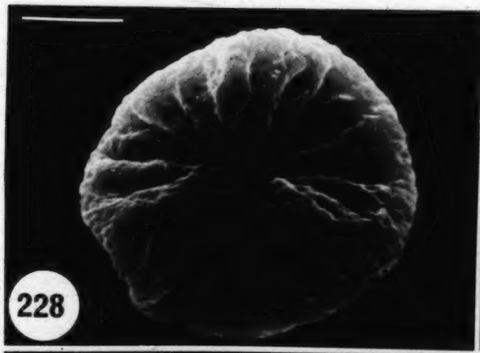

227

Figures 228-231. Encalypta microstoma **Variation in Spores** (cont'd.). Proximal Surface.

Fig. 228. Scale=10 µm.

Fig. 229. Scale=4 µm.

Figs. 230-231. Scale=10µm.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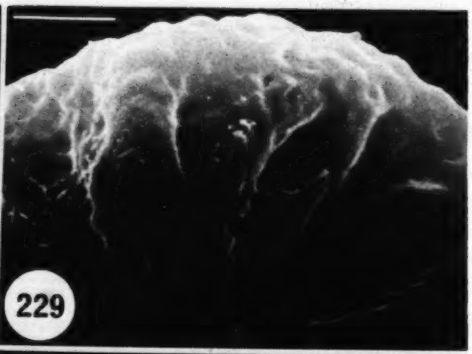
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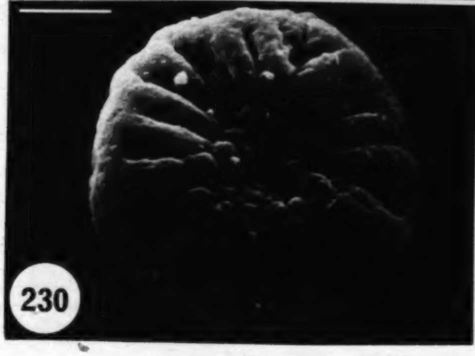
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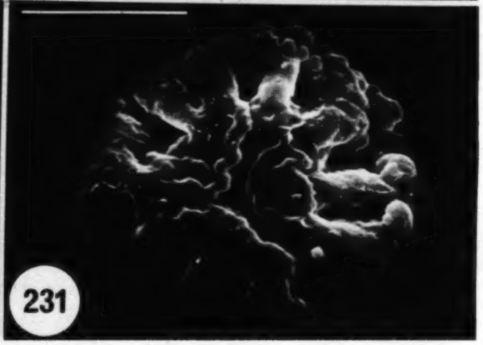

231

calyptra is different; in *E. ciliata* the cylinder is broader, which makes the rostrum appear narrower than in *E. microstoma* (Fig. 233). The length of the rostrum of *E. ciliata* is quite consistently 1/3 the overall length of the calyptra, while in many populations of *E. microstoma* the rostrum is only 1/4 the total length. Capsules of *E. ciliata* are distinctly constricted just below the mouth and abruptly narrowed to the seta; in contrast, those of *E. microstoma* are contracted to the mouth (only rarely constricted and then less distinctly so than in *E. ciliata*) and more gradually narrowed into the seta (Fig. 234). A well-developed peristome is characteristic of *E. ciliata*, but absent in *E. microstoma* (when a fragmentary peristome does occur, it is always hyaline, never with dark-orange teeth as in *E. ciliata*). The setae in populations of *E. ciliata* are generally longer (up to 15 mm, while those of *E. microstoma* are only up to 6 mm), although they are shorter in some alpine populations of *E. ciliata*. However, in a mixed collection of *E. ciliata* and *E. microstoma*, setae of the former taxon vary from 5-7 mm in length, while those of the latter are 4 mm. In populations of *E. ciliata*, the leaves are mucronate and the margins are always narrowly recurved in the lower 1/2 to 2/3, in contrast to the muticous leaves with plane margins of *E. microstoma*. Leaves of *E. ciliata* tend to be longer and therefore are more strongly contorted than those of *E. microstoma*. Microscopically, *E. microstoma* and *E. ciliata* are different in the transverse section of the capsule wall with the outer tangential walls of the exothecial cells in *E. ciliata* strongly and evenly thickened in contrast to the strong, localized thickenings characteristic of *E. microstoma*.

The vast majority of populations of *E. ciliata* are concentrated in the Northern Hemisphere north of 30°N. These are relatively uniform in the character-states discussed above, except that "aberrant" capsules (see below) occur quite frequently. However, in populations of *E. ciliata* from the Southern Hemisphere and south of 30°N in the Northern Hemisphere, there is considerable variation in calyptra, capsule, peristome and leaf structure (see discussion of Variation under *E. ciliata*). This variability is exemplified in collections from Mexico and South America. Some of these populations mimic *E. microstoma* in calyptra and capsule shape, and the lack of a peristome (Figs. 232, 235). As well, the calyptra fringe is pale brown in many populations and, in some, is even darker brown than in *E. microstoma*. Populations with muticous leaves are of sporadic occurrence. However, these "Southern Hemisphere" populations of *E. ciliata* are

Figures 232-236. Encalypta microstoma and E. ciliata Scale=1 mm.

Fig. 232. Encalypta ciliata. Capsule from Mexican population.

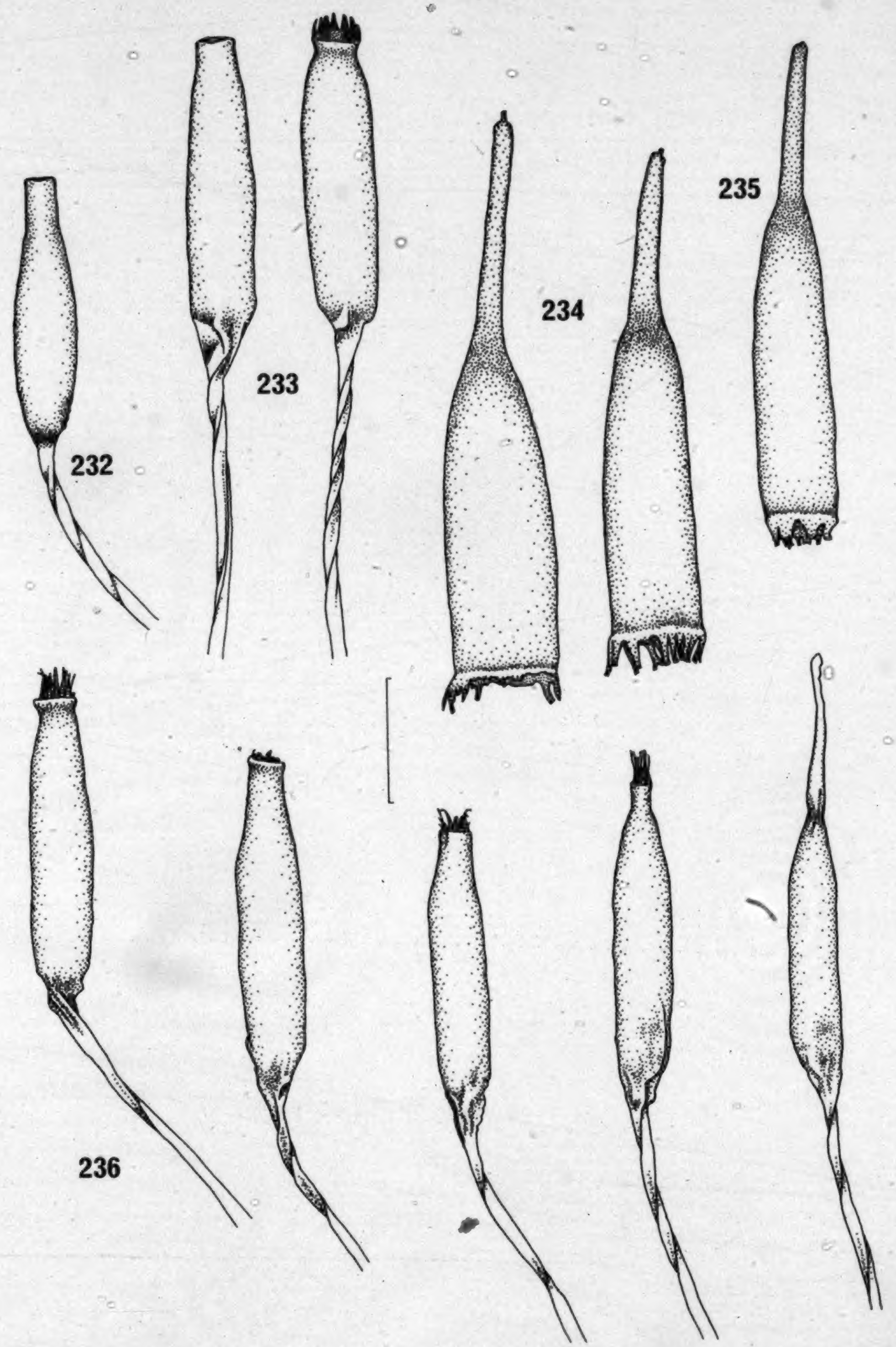
Figs. 233-234. Encalypta microstoma (left) and E. ciliata (right).

Fig. 233. Capsules.

Fig. 234. Calyptrae.

Fig. 235. Encalypta ciliata. Calyptra from Mexican population.

Fig. 236. Encalypta ciliata. Capsules from single population to illustrate gradation from extremely 'aberrant' capsule (right) to 'normal' capsule (left).



consistently differentiated from *E. microstoma* by recurved leaf margins.

The identity of *E. microstoma* has been obscured because the forms of its capsule parallel some of those that occur relatively frequently in populations of *E. ciliata*. Generally, *E. ciliata* is characterized by a well-developed peristome, and smooth, cylindric and turgid-looking capsules with a distinct constriction just below the mouth, the diameter of the latter being more-or-less equal to that of the capsule below the constriction (Fig. 236 - left). Such capsules are quite distinct from those of *E. microstoma*; however, there are populations of *E. ciliata* that are characterized completely or in part by capsules with quite a different structure, which I refer to as "aberrant". The range of structural variation of "aberrant" capsules of *E. ciliata* is considerable and grades imperceptibly into capsules with structure typical for *E. ciliata*, described above. The forms that resemble capsules of *E. microstoma* represent only a small portion of this variability.

Capsules of *E. ciliata* that represent the most extreme expression of "aberrant" capsules are cylindric and more-or-less smooth and turgid-looking, some are tapered distally, and there is always a distinct constriction or an abrupt contraction just below the minute mouth, the latter being considerably less than the diameter of the central part of the capsule (Fig. 236 - right and extreme right). In some instances, the capsule is cleistocarpous (with the operculum remaining attached and no line of dehiscence apparent) (Fig. 236 - extreme right); in others, the operculum dehisces, but the peristome teeth are very irregular or lacking altogether (Fig. 236 - right). The mouth is similarly very irregular. Often "aberrant" capsules occur intermixed in populations that have capsules of the shape typical for *E. ciliata*, and in a few specimens a complete structural gradient from the extreme "aberrant" capsules to those characteristic of *E. ciliata* occurs (Fig. 236). Some of these less strikingly "aberrant", intermediate forms are virtually indistinguishable from capsules of *E. microstoma*, except for the presence of a peristome (Fig. 236 - centre).

The occurrence of intergrading forms between typical *E. ciliata* capsules and "aberrant" capsules within individual populations indicates that the latter probably do not represent a habitat modification. In all other features, the plants with "aberrant" capsules are indistinguishable from those typical of *E. ciliata* in the narrowest sense. The abnormal appearance of the extreme "aberrant" capsule forms suggests that such capsules may be the product of some developmental irregularity. While there may be some genetic basis causing this irregularity, it is clear that such forms are not in any way genetically isolated from "normal" *E. ciliata*. Also, similarly "aberrant" capsules occur in such other species of *Encalypta* as *E. affinis*, *E. alpina* and *E. brevicolla*, and I have observed what might be interpreted as "aberrant" capsules in a few populations of *E. microstoma* (Fig. 219 – extreme right). This indicates that the genetic potential for the formation of such capsules traverses interspecific as well as infraspecific boundaries; therefore, they should not be given any formal nomenclatural recognition. In contrast, the consistent structural differences and the occurrence of mixed populations indicate genetic isolation of *E. microstoma* and *E. ciliata*. There should be no doubt that these taxa are distinc at the specific level.

Encalypta brevipes resembles *E. microstoma* in gymnostomous capsules and short setae. However, *E. brevipes* is differentiated by the extremely short, stubby rostrum of the calyptra and the leaves with very long hair-points. Microscopically the basal cells of the leaves are less distinctly defined because the transverse walls are pale-yellow. The spore sculpture is quite different and consists of a distinctly-defined verrucose reticulum.

Description: *Plants* to 20 mm tall, olive-green to bright-green above, brown to blackish below; ± branched. *Stem* in transverse section with central strand absent. *Brood bodies* absent. *Axillary hairs* sparse. *Leaves* when dry incurved and ± twisted, laminae plane to slightly undulate and incurved to conduplicate; 2.3–4.3 mm long, 1.0–1.4 mm wide, oblong to ovate-, obovate- or elliptic-oblong to elliptic, apex muticous and broadly acute to acute or very shortly acuminate; *margins* plane. *Costa* subpercurrent or ends well below apex, abaxial surface prominently keeled, shiny and yellow to olive-yellow or brown, sparsely papillose distally, papillae low and rounded; in transverse section 2–3 rows ventral cells, begleiters undifferentiated, 2–3 rows of stereids. *Upper laminal cells* (7)12–14(18) μm wide, (7)12–14(20) μm long, with 3–6 papillae per cell, some indistinctly "c"-shaped; *upper marginal cells* 9–14 μm wide, 7–10 μm long; *transitional cells* papillose to basal cells on abaxial surface, papillae as on upper cells, on adaxial surface smooth well above basal cells; *basal laminal cells* 16–50 μm long, 9–20 μm wide, prominent, transverse walls dark-orange, longitudinal walls hyaline, superficial walls smooth, entire to irregularly ± perforated. Goniautoicous. *Perichaetial leaves* sheath-like and broadly ovate-lanceolate to oblong-lanceolate, apex muticous and acute to shortly acuminate; costa ends in apex; *perigonial leaves* 0.7–0.8 mm long, sheath-like and oblong to very broadly oblong, abruptly narrowed to shortly acuminate apex or to lanceolate upper portion and acute apex; *perigonial paraphyses* with upper cells entire, walls smooth.

Seta 2.5–6.0 mm long, erect to slightly flexuose, slightly twisted sinistrorsely below, ± strongly twisted dextrorsely in upper part, shiny and yellow below and red just at base of capsule to dull orange or brownish with age; in transverse section 145–185 μm in diameter. *Capsule* 1.2–3.0 mm long, when dry narrowly cylindric to cylindric, ± tapered distally and in some ± contracted ± below mouth to indistinctly constricted just below slightly oblique, ± narrow mouth, slightly constricted basally, then gradually tapered to seta, abruptly contracted to seta in very few populations, smooth, yellow to copper-yellow with rim red or undifferentiated; when young greenish-yellow with rim red or undifferentiated; when old ± wrinkled, collapsed and longitudinally split, dull-orange; *exothecial cells* 40–95 μm long, 12–20 μm wide, in ± regular, longitudinal rows, in transverse section walls strongly thickened on superficial and adjacent radial walls, 9 μm thick; *rim cells* in 2–5 rows, 5–23 μm long, 10–20 μm wide, walls ± thickened; *stomata* scattered, superficial, prominent ring of thickened walls outline guard cells, 32–53 μm long, 23–41 μm wide. *Peristome* absent in most populations, when present in 1 concentric layer, vestigial, teeth 16, ± erect, ± truncate, hyaline or white, outer surface with 1 vertical row of cell plates, sparsely irregularly papillose to ± smooth, inner surface with 2 vertical rows of cells plates, smooth. *Operculum* convex to slightly concave, and short-rostrate, 1.0–1.2 mm long. *Annulus* undifferentiated. *Spores* orange, heteropolar, in polar view radially symmetric and circular, 32–41 μm, in equatorial view polarly asymmetric and plane-convex, 23–28 μm X 32–41 μm, proximal surface with numerous radial plicae and ± distinct trilete mark, in some ± irregularly puckered around trilete mark; on distal surface 5–7 ± radial plicae extend from ± distinct rim bordering ± distinct central pit, in some pit, rim and plicae are overlain by verrucose reticulum; both surfaces are minutely, ± distinctly pitted. *Calyptra* 3.2–5.3 mm long, extends well below capsule, cylindric, gradually tapered above and then rather distinctly, but only slightly contracted to slightly curved, erect in very few, thick rostrum that is 1.0–1.8 mm long, base of cylinder slightly expanded horizontally to obliquely, fringed, segments narrowly to broadly trapezoidal, pendent to spread, calyptra dark-golden to dark-brown distally with dark-brown, pale brown in few populations, fringe, shiny and opaque, ± smooth; in transverse section cylinder with 3 rows cells with very thick walls, fringe with 1 row of cells, walls exceptionally thickened in 2 layers, outer yellowish, inner hyaline; in superficial view fringe cells short- to long-oblong. Chromosome number unreported.

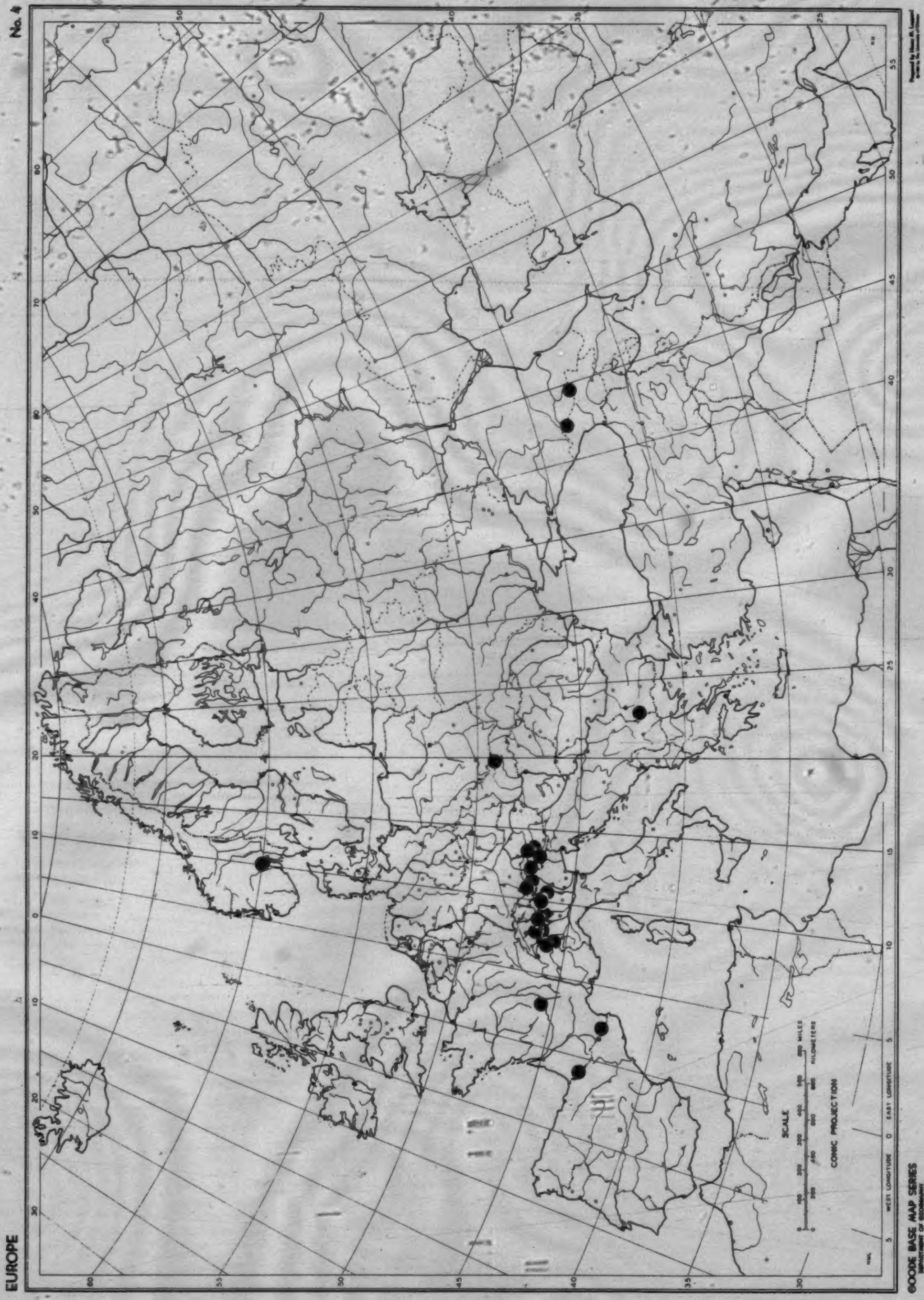
Habitat: Populations of E. microstoma have been quite frequently collected with plants of E. ciliata intermixed, which suggests that these two closely related species have very similar habitat preferences. Although populations of E. ciliata occur in alpine and arctic tundra, they are more frequently associated with more mesic, forested habitats at lower elevations. Therefore, this species is widespread outside of mountainous regions. It is apparent from the distribution of E. microstoma that it, in contrast, is restricted to montane habitats. The data on collection labels of E. microstoma are meagre, but elevations of 1,000 to 2,700 metres have been recorded so it can be inferred that populations occur from below treeline up into alpine tundra. I have collected E. microstoma at two different localities in the Swiss Alps; one was in alpine tundra at approximately 2,700 metres where it occurred on a dry, rocky slope with west aspect, and the other was at 2,100 metres in the upper subalpine Larix europaea DC. zone where it occurred on a dry rock outcrop with west aspect. The apparent dryness of both habitats was notable by comparison to E. ciliata. The latter species tends to grow in slightly mesic habitats where there will be a little intermittent seepage. At the first locality E. microstoma was growing on soil beneath the edge of a small solifluction terrace where it was well protected by an overhanging tuft of Festuca haleri All. and by surrounding granite outcrops. In the immediate area large mounds of Silene acaulis L. were a prominent feature indicative of the exposed nature of the vegetation, which also included Agrostis rupestris All., Alchemilla alpina (L.) Scopoli, Juncus trifidus L., Phyteuma hemisphaerica L. and Saxifraga bryoides L. Tortella tortuosa (Hedw.) Limpr. was relatively abundant on soil in the vicinity. At the second locality, E. microstoma was also well-protected, growing back in the crevices of the siliceous outcrop with Tortella tortuosa, and in more exposed positions on the face of the rock with Pterigynandrum filiforme Hedw. Particularly indicative of the xeric nature of this habitat was the dominance of Juniperus communis L. bushes. Also present were Campanula cochlaerifolia Lam., Minuartia laricifolia (L.) Schinz et Thell., Saxifraga paniculata Miller and Sempervivum arachnoidum L. The relative dryness of both these habitats and the restriction of E. microstoma to montane regions may indicate a shift in some aspects of the habitat preferences of this species away from those of E. ciliata.

Another important feature of the habitat of E. ciliata is that this species frequently grows where the substrate is siliceous, although it also occurs on calcareous substrates. In western North America the pH of the soil on which populations of E. ciliata were growing ranged from 5.3 to 7.1 with a mean of 6.3 (see Habitat under E. ciliata). Species that are frequently associated with E. microstoma include such indicators of more siliceous conditions as Bartramia ithyphylla Brid., while such others as Eurhynchium pulchellum (Hedw.) Jenn. and Myurella julacea (Schwaegr.) B.S.G. are generally associated with calcareous conditions. As noted above, the rocks at both the localities where I collected E. microstoma were siliceous, and pH of the soil was 5.7 at the first locality and 5.8 at the second. Therefore, populations of E. microstoma probably occur under very similar conditions to those of E. ciliata with regard to substrate-type.

Distribution: Encalypta microstoma has a relatively restricted distribution across the montane regions of central and southern Europe from the Pyrénées Atlantiques and the Pyrénées Orientales, and the Massif Central in France, through the Swiss, Austrian and northern Italian Alps, the High Tatras of Czechoslovakia, and somewhat disjunct in the Rila Mountains of Bulgaria and the Caucasus Mountains. An additional locality disjunct in southeastern Norway (Hagen 27.7.90 - O) was tentatively reported in Horton (1981c), but upon further consideration I see no particular reason to doubt the validity of the locality indicated on this specimen (Fig. 237).

Coker (1918) reported E. microstoma (as E. laciniata var. microstoma) to occur in North America in "Northern New York and in alpine regions of the Rocky Mountains.".

Figure 237. Distribution of *Encalypta microstoma*.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No. 4
SCALE
MILES
KILOMETERS
CONIC PROJECTION
WEST LONGITUDE
EAST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

However, her description is of "aberrant" capsules of *E. ciliata*. I have seen no specimens of *E. microstoma* from North American localities.

Encalypta microstoma is a rare species, endemic to central and southern Europe. In each of the herbaria examined, there exist only a few specimens, and less than 15 in total have been collected since 1950 (in the herbaria that I have had access to). The concentration of collections from localities in central and southern Austria-Switzerland and northern Italy indicates that this region can be considered the centre of the range of *E. microstoma*. It is to be expected from Jugoslavia and possibly Hungary. Hopefully, the occurrence of *E. microstoma* in Scandinavia will be reaffirmed in the future.

By comparison to most other species of *Encalypta*, the distribution of *E. microstoma* is markedly restricted. For example, *E. ciliata* and *E. rhaptocarpa* are relatively common and widespread in montane and boreal habitats of the Northern Hemisphere. Even such species as *E. brevipes*, *E. brevicolla*, *E. longicolla*, *E. mutica* and *E. spathulata*, all of which have been suggested by various authors to have relictual distribution patterns, occur both in North America and Eurasia. Only two recently described species, *E. vittiana* Horton and *E. flowersiana* Horton (Horton 1979b), appear to have distributions as restricted as that of *E. microstoma*. *Encalypta vittiana* is known from northwestern North America in Alaska, the Yukon Territory and western Northwest Territories, while *E. flowersiana* has been reported from Guatemala, Haiti and Texas. The restriction of each of these three species to a single continent, in contrast to almost all other species of *Encalypta*, suggests that *E. microstoma*, and *E. flowersiana* and *E. vittiana* have evolved relatively recently.

Phylogenetic Relationships: Clearly, *E. microstoma* is most closely related to *E. ciliata*. The yellow tones that characterize plants of *E. ciliata* are paralleled in *E. microstoma*. While there are some differences in character-states of the calyptra and capsule, as noted in Diagnosis and Differentiation, overall the structure is very similar. Leaves of *E. microstoma* are broad, as are those of *E. ciliata*, with a smooth, shiny costa and the structure of the basal cells is virtually identical in these two species.

Specimens Examined: ALTA (2), BM (7), BP (8), DUIS (3), F (1), FI (13), G (4), H (4), H-Br

(5), H-Sol (3), Priv. Herb. D. G. Horton (3), KRAM (1), L (1), LAU (1), M (8), NY (1), O (3), S (10), W (17).

ENCALYPTA RHAPTOCARPA Schwaegrichen,

Spec. Musc. Suppl. 1(1): 56, fig. 16. 1811.

Figs. 238-242.

Types: "Legi ad nives alpis Carinthiae *Heiligenbluter Tauern* cum Hypno *iulaceo*, aliis locis similibus Gebhard invenit, Augusto fructiferum." (Lectotype: "Encalypt. rhaptocarp. ? [illegible]" G-Hedw.-Schwaegr.!).

Diagnosis: One of the most prominent features that defines *E. rhaptocarpa s. str.* is the dark-red, longitudinal ribs on the capsule. Also characteristic is the opaque, golden calyptra that is plain by comparison to those of many other species of *Encalypta*. It is dull, the base of the cylinder is either entire or erose, and the relatively long (up to 2 mm), well-defined rostrum is broad and somewhat enlarged distally. There is a well-developed, single peristome of dark-red to orange teeth and a preperistome occurs not infrequently. The orange to dark-red seta is of moderate length (generally 5-8 mm long) and is more-or-less twisted dextrorsely at the base of the capsule. The leaves are characterized by a long, hyaline hair-point and on the abaxial surface in the upper part by a smooth, shiny costa that is narrow and inconspicuous. The costa is green or golden above to dark reddish-brown basipetally. Dark-red to orange longitudinal and transverse walls characterize the distinctly differentiated basal cells and the uppermost of these form a line that is more-or-less perpendicular to the costa. On the distal surface of the spores are numberous, large verrucae, while the proximal surface is characterized by narrow, radial plicae with some granules centrally.

Variation: Many species of *Encalypta* are differentiated by a unique exospore sculpture. However, all species in the *E. rhaptocarpa-E. vulgaris* complex, including *E. armata*, *E. asperifolia*, *E. flowersiana*, *E. intermedia*, *E. rhaptocarpa*, *E. spathulata*, *E. vittiana* and *E.*

Figures 238-241. Encalypta rhaptocarpa Spores.

Figs. 238 & 240. Distal surface.

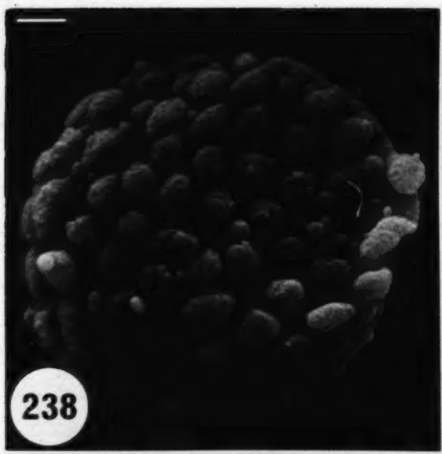
Fig. 238. Scale=5 µm.

Fig. 240. Scale=1 µm.

Figs. 239 & 241. Proximal surface.

Fig. 239. Scale=5 µm.

Fig. 241. Scale=1 µm.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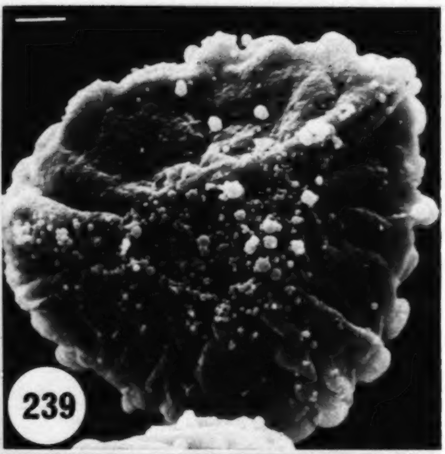
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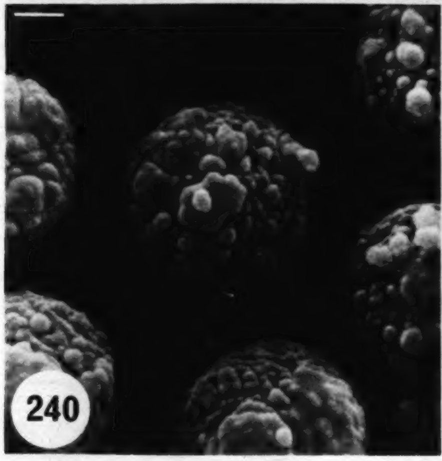
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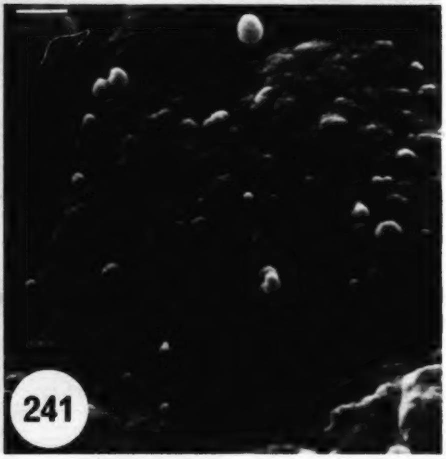
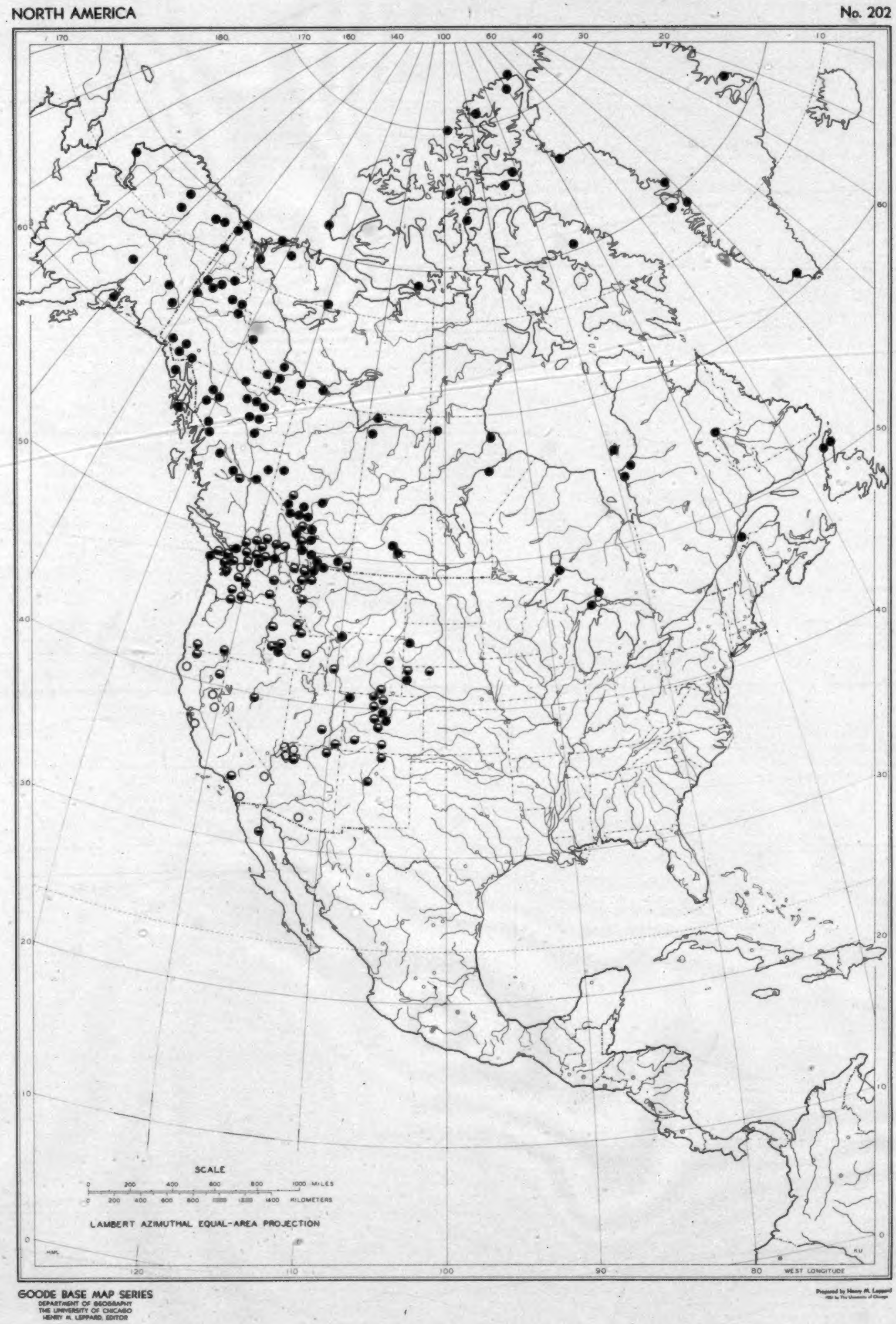

241

vulgaris, are characterized by heteropolar spores with large, warty protuberances on the distal surface (for purposes of this discussion, warty is used in a slightly broader sense here to include the warty-vermiform spores of *E. flowersiana*). The uniformity in spore-type that characterizes the taxa in this complex is in sharp contrast to the wealth of variation that occurs in other character-states. A myriad of modifications reflects various combinations of numerous character-states that occur in different populations (Table 4). Many of these modifications have been given nomenclatural recognition and this has given rise to a not inconsiderable list of epithets (see van der Wijk *et al.* 1962, 1969). Despite the variability that characterizes these taxa, I feel that my understanding of most of these is good enough to make a valid taxonomic judgement (see treatments of *E. armata*, *E. asperifolia*, E. flowersiana, *E. spathulata* and *E. vittiana*). However, the taxonomic status of *E. rhaptocarpa*, *E. intermedia* and *E. vulgaris* is open to question. I find that I am unable to satisfactorily define the limits of these three taxa, particularly of *E. rhaptocarpa* and *E. vulgaris*.

Encalypta rhaptocarpa s. str. and *E. vulgaris s. str.* are readily differentiated on the basis of several characteristics. Most reliable of these are presence (*E. rhaptocarpa*) or absence (*E. vulgaris*) of ribs on the capsule; presence (*E. rhaptocarpa*) or absence (*E. vulgaris*) of a peristome; hair-pointed leaves in *E. rhaptocarpa* versus muticous leaves in *E. vulgaris*; an inconspicuous, green costa in *E. rhaptocarpa* versus a prominent, golden-brown costa in *E. vulgaris*; and basal cells prominent with red or orange walls (*E. rhaptocarpa*) or basal cells inconspicuous with yellow to pale-orange walls (*E. vulgaris*). In North America, *E. vulgaris s. str.* is more-or-less restricted to California and Arizona (Fig. 242), while *E. rhaptocarpa s. str.* occurs in boreal regions across the Continent from Newfoundland and Labrador to Hudson Bay and the Great Lakes, across Manitoba, Saskatchewan and Alberta, through British Columbia. Along the Cordilleran axis it has been found in the Brooks Range in northern Alaska and the British Mountains in northern Yukon Territory southward through Alaska, the Yukon and the western Northwest Territories to Colorado. In the Arctic, *E. rhaptocarpa* has been collected at widespread localities including the Mackenzie Delta, Great Bear Lake and on Banks, Victoria, Somerset, Baffin, Bathurst, Cornwallis, Devon, Meighen and Ellesmere Islands and in Greenland (Fig. 242). In Europe, the general pattern of distribution is the same with *E. rhaptocarpa* predominating

Figure 242. Distribution of *Encalypta rhaptocarpa* (solid circles), *E. vulgaris* (open circles) and Intermediate Populations (half circles) in North America.


NORTH AMERICA
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SCALE
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0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
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110
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WEST LONGITUDE
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TABLE 4. Occurrence of Character-States in Problematical Taxa Belonging to the *Encalypta rhaptocarpa* - *E. vulgaris* Complex

	TAXA				
CHARACTER AND CHARACTER-STATES	*Encalypta spathulata*	*Encalypta rhaptocarpa*	*Encalypta intermedia*	*Encalypta vulgaris*	*Encalypta asperifolia*
Calyptra					
- pale-golden and transparent	XX	O			
- golden to brown distally and transluscent	O	XX	XX	XX	XX
-Rostrum - short (0.8-1.0mm)	XX		XX		O
-longer (1.0-2.0mm)		XX		XX	XX
-Fringe-well-differentiated	XX				XX
- ill-defined	X				X
- absent	O	XX	XX	XX	
Capsule					
- smooth				XX	X
- longitudinally plicate	XX	XX	XX	X	X
- deeply longitudinally furrowed		XX	XX		X
- ribs dark	X	XX	XX		X
- ribs pale	X	XX	XX	X	X
- ribs absent		XX		XX	X
Peristome					
- ±well-developed, dark-red to pink		XX	X		
- vestigial, white to hyaline	X	X	X	X	
- absent	XX	X	XX	XX	X
Seta					
- short (1-6 mm)	XX	X	XX	X	X
- longer (4-8 mm)	O	XX		XX	
- dark-red to red	XX	XX	X	X	
- orange		XX	X	XX	
- yellow				X	

TABLE 4. Continued

CHARACTER AND CHARACTER-STATES	TAXA Encalypta spathulata	 Encalypta rhaptocarpa	 Encalypta intermedia	 Encalypta vulgaris	 Encalypta asperifolia
Leaf Apex					
– muticous	X(lower lvs.)	X	XX	XX	XX
– apiculate				X	
– hair-pointed	XX	XX	X		
Costa					
– green		XX	XX	X	
– golden	XX	X	X	XX	XX
– dark-brown	XX		X	XX	XX
– prominent on abaxial surface near apex	XX		X	XX	XX
– inconspicuous on abaxial surface near apex		XX	XX	O	
– shiny	XX	X	X	XX	XX
– dull			XX		
– ends well below apex	X(lower lvs.)		XX	X	
– ends near apex		X	X	XX	XX
– excurrent	XX	XX	X	X	
Basal Laminal Cell Walls					
– dark-red		XX			X
– orange	X	X	X	X	X
– yellow	X	X	X	X	

X indicates occurence of characteristic
XX indicates characteristic most commonly occurring in populations of a particular taxon
O indicates exceptional occurrance within population of a particular taxon

in more northerly regions and *E. vulgaris* more common in southerly areas (although the latter does occur as far north as Scandinavia).

In addition to the populations of *E. rhaptocarpa s. str.* and *E. vulgaris s. str.*, there occur, in both North America and Europe, populations characterized by modifications of the character-states that otherwise define *E. rhaptocarpa* and *E. vulgaris*. Such populations are not uncommon within certain geographic regions in North America (Fig. 242) and the modifications are of characteristics that are critical for differentiating *E. rhaptocarpa* and *E. vulgaris*. In *E. rhaptocarpa*, which appears to be subject to more variability than *E. vulgaris*, there is a loss of ribs on the capsule, a poorly-developed or vestigial peristome or even the complete absence of a peristome, lack of an excurrent costa, the costa more prominent on the abaxial surface of the leaves, and basal cells with pale colored walls (Fig. 243, Table 4). In *E. vulgaris*, modifications include the occurrence of plications and faint ribs on the capsule, a vestigial peristome, leaves with an excurrent costa or with the costa inconspicuous on the abaxial surface, and basal cells with slightly darker walls (Fig. 243, Table 4). The expression of this variability is primarily interpopulational; individual populations are generally more-or-less uniform in structure, and there appears to be no correlation in the occurrence of particular character-states (Fig. 243). For example, a population of *E. rhaptocarpa* may have capsules that lack dark-red ribs, but the peristome is well-developed with dark-red teeth. Some of the forms of *E. rhaptocarpa* and *E. vulgaris* represent such a blend of the characteristics of these two taxa that it is difficult to give a satisfactory determination. Similar structural variation also occurs in populations of *E. rhaptocarpa* and *E. vulgaris* in Europe. For example, in the type specimen of *E. rhaptocarpa*, the peristome teeth are pale-orange and not as well-developed as in 'typical' *E. rhaptocarpa*. It is possible that the structural complexity that confuses the distinction between these two taxa is the result of intergradation. If there is a correlation between distribution and the occurrence of intermediate populations in Europe as there is in North America (Fig. 242), it might be that it is more realistic to consider *E. rhaptocarpa* and *E. vulgaris* as subspecies.

Historically, *E. rhaptocarpa* and *E. vulgaris* has been regarded as distinct species with many infraspecific taxa. Lawton (1971) treated *E. rhaptocarpa* as a variety of *E. vulgaris*, but her concept of the latter almost certainly included *E. intermedia* (see

Figure 243. Combinations of Character-States That Occur in Populations Intermediate Between *Encalypta rhaptocarpa* (top) and *E. vulgaris* (bottom) in Western North America.

Three solid triangles indicate a well-developed peristome; one open triangle indicates the lack of a peristome.

Three solid ovals indicate prominent capsule ribs; one open triangle indicate the lack of ribs.

Two solid squares indicate the presence of hair-points on the leaves; one open square indicates muticous leaves.

One solid circle indicates an inconspicuous costa that does not a keel on the abaxial surface of the leaf; two open circles indicates a prominent, strongly protruding costa that forms a distinct keel on the abaxial surface.

INTERMEDIATE POPULATIONS: Intergradation of Character-states

	Peristome	Capsule ribs	Hair points	Costa protrudance
Yukon: Ogilvie Mtns. 66° 139°	▲▲▲	⬮⬮⬮	■■	●
B.C.: Saltspring Is. 48° 123°	◭	⬮	⬓	○
Wash.: Skagit Co. 48° 122°	◭	⬯	⬓	○◒
B.C.: Lytton 50° 121°	▲▲△	⬮⬮⬮	■■	●
B.C.: Lillooet 50° 121°	△	◒	■⬓	●
B.C.: Manning Park 49° 120°	△	⬮◒	■■	●
Wash.: Chelan Co. 48° 120°	△	◒	■	○
Wash.: Chelan Co. 48° 120°	▲	⬮⬮⬮	■■	●
Wash.: Kittitas Co. 47° 120°	△	⬯	■■	●
B.C.: Oliver 49° 119°	△	⬯	■	○
B.C.: Okanagan Valley 49° 119°	△	⬯	■■	●
B.C.: Osoyoos Lake 49° 119°	▲▲	⬮⬮⬮	■■	●
B.C.: Revelstoke 50° 118°	△	⬮◒	■■	●
B.C.: Rosebery 50° 117°	▲	⬯	■	◒
B.C.: New Denver 49° 117°	△△	⬯⬯	■■	●
Wash.: Spokane Co. 48° 117°	△	⬯	■	○○
Mont.: Lincoln Co. 48° 115°	△	⬯	□	●
Mont.: Flathead Co. 49° 114°	◭	⬮⬮⬮	■■	◒
Mont.: Lake Co. 48° 114°	△△	⬮⬮⬮	■■	●
Alta.: Cypress Hills 50° 110°	▲▲△	⬮⬯	■■	●
Arizona: Grand Canyon 36° 112°	△	⬯	□	○○

discussion of Variation under *E. intermedia*). In 1910, Hagen discussed the variation and apparent intergradation among taxa in the *E. rhaptocarpa–E. vulgaris* complex, but he recognized most as distinct at the specific level. He explained that "Si je ne tire pas la conséquence de cette démonstration, si je ne réunis pas toutes ces formes en une seule espèce sous le nom le plus ancien d'*E. extinctoria*, [=*E. vulgaris*] c'est par pure concession à l'opinion généralement répandue, mais j'aime à croire que cette opinion s'ébranlera peu à peu, et que le temps viendra où l'on pourra effectuer cette réforme sans éveiller de susceptibilités.". I am at present similarly reluctant to instigate such a change, but my reluctance is related more to my feeling that I do not yet have an adequate understanding of the problem than to a concern that a change might not be generally accepted. Studies are now in progress to determine if the intermediate populations of *E. rhaptocarpa* and *E. vulgaris* reflect intergradation between these taxa or if the intermediates actually represent expressions of two highly polymorphic species.

ENCALYPTA VITTIANA Horton,

Bryologist 82: 369, figs. 1–10. 1979.
Figs. 244–249.

Types: "CANADA: Yukon Territory, Bonnet Plume Rng., slopes above northwest shore of Pinguicula L., 64°42'N; 133°27'W, elev.: 824–967 m. Alpine tundra below limestone outcrops; on *Dryas integrifolia* overhangs at the lip of solifluction terracettes, *D. G. Horton & D. H. Vitt*, 10 July, 1976 (holotype – ALTA, isotype – priv. herb. D. G. Horton); *Horton 5794* (paratype – CANM). Northwest Territories, Logan Mts., southeast side of unnamed lake, 62°34'N; 128°31'W, *Horton 14467* (paratypes – ALTA, NY); MacKenzie Mts., northernmost end of Nahanni Rng., 62°13'N; 123°22'W, *Horton 10452* (paratype – ALTA). UNITED STATES: Alaska, Brooks Range, Endicott Mts., Anaktuvuk Pass, along Contact Cr., 68°11'N; 151°52'W, *Horton 8582* (paratypes ALTA, priv. herb. of D. G. Horton).".

Diagnosis and Differentiation: *Encalypta vittiana* is characterized by golden-brown to dark-brown calyptrae with a broad, curved rostrum and a long, pale fringe; by strongly, longitudinally furrowed capsules with a well-developed, single peristome; by polar spores with rounded, warty protuberances on the distal surface; and by hair-pointed leaves. The plants are variable in size; some populations consist of very small plants, while those of others are considerably larger. This newly described species is most closely related to *E. rhaptocarpa*. Character-states of capsules, spores and leaves, as well as microscopic features of laminal cell structure of the two species are indistinguishable. However, *E. vittiana* is distinctly differentiated from *E. rhaptocarpa* by the clearly defined fringe at the base of the calyptra. Populations of *E. rhaptocarpa* lack a fringe at the base of the calyptra; it is either entire or erose. Other features of the calyptra, which are less definitive, but nevertheless useful, for differentiating between these two species, are the length of the rostrum, which is 1.0 to 1.2 millimetres long in *E. vittiana*, but may be up to 2.0 millimetres long in *E. rhaptocarpa*; the rostrum of *E. vittiana* is invariably curved, in *E. rhaptocarpa* it may be erect or curved; the cylinder of the calyptra of *E. vittiana* is often dark-brown, while that of *E. rhaptocarpa* is generally golden-brown. The calyptra of *E. vittiana* is strikingly similar to that of *E. longicolla* Bruch, and populations of *E. vittiana* with spear-stage sporophytes enclosed in calyptrae are difficult to distinguish from those of *E. longicolla*. Both species have hair-pointed leaves, although those of *E. longicolla* are narrower than those of *E. vittiana*. *Encalypta longicolla*, like *E. vittiana*, is characterized by more darkly colored calyptrae than are most species of *Encalypta*, and it too has a broad, curved rostrum, which is approximately one millimetre long. However, the cylinder of the calyptra of *E. vittiana* is elliptic-cylindric in shape, while that of *E. longicolla* is cylindric. Also, the cylinder of the calyptra of *E. longicolla* tends to be longer than is that of *E. vittiana*.

Description: *Plants* variable, 1-2 mm tall in some populations, to 10 mm tall in others, glaucous-green to olive-green above, brown below, ± branched. *Stem* in transverse section with central strand distinct in some populations, cells small, walls thin. *Brood bodies* absent. *Axillary hairs* sparse. *Leaves* when dry incurved, slightly twisted in some populations, laminae inflexed to plane or conduplicate; 1.7-2.5(3.0)

Figures 244-248. __Encalypta__ __vittiana__. Scale=1 mm.

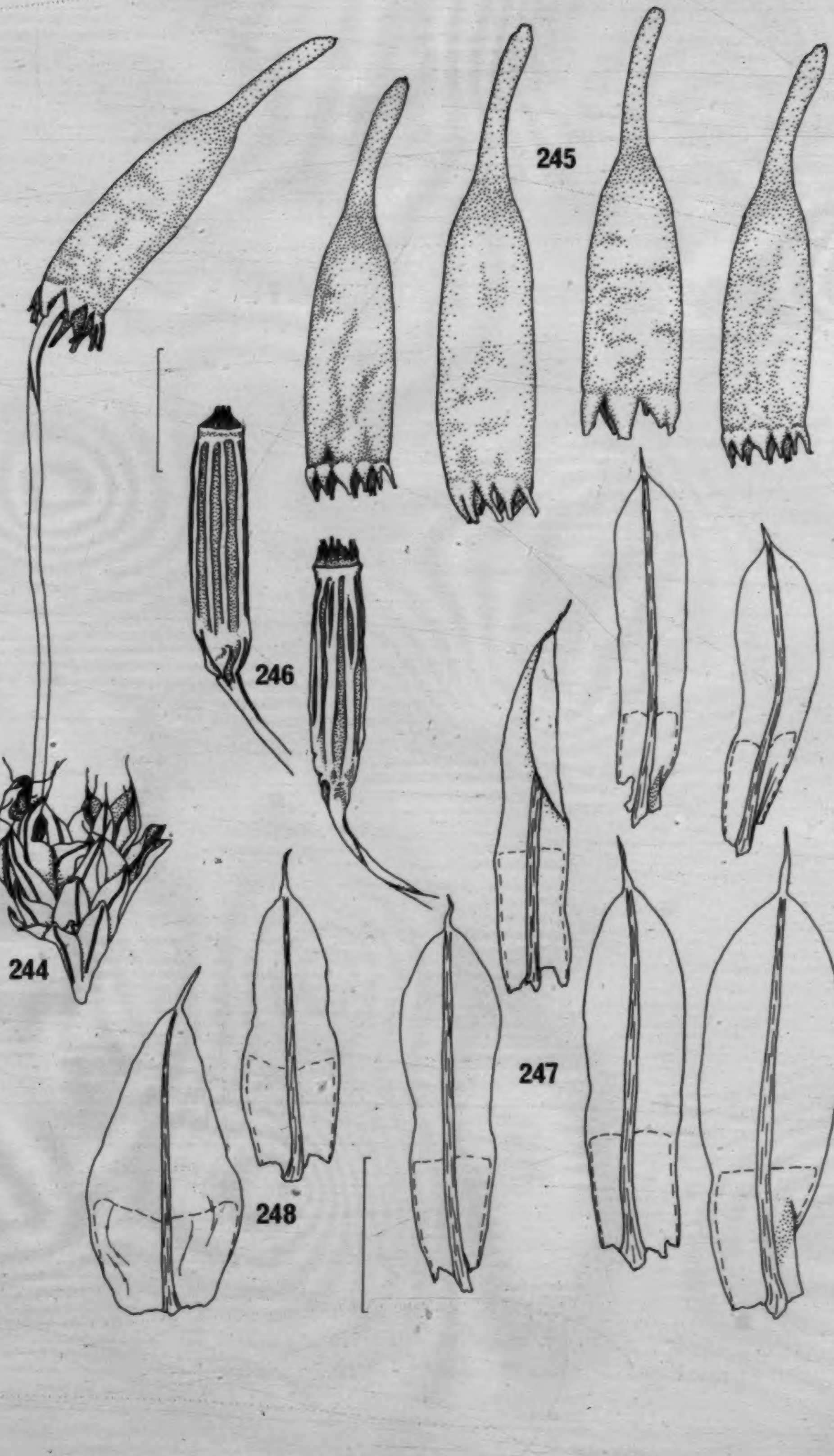
Fig. 244. Habit

Fig. 245. Calyptrae.

Fig. 246. Capsules.

Fig. 247. Vegetative leaves.

Fig. 248. Perichaetial leaves.



mm long, 0.5–0.7(0.8) mm wide, oblong to narrowly oblong or narrowly lingulate, apex broadly acute, hair-poin margins plane. Costa excurrent, abaxial surface orange on lower leaves to transluscent green on upper leaves, strongly papillose to sparsely prorulose above basal cell region; in transverse section 2–3 rows ventral cells, begleiters undifferentiated, 2–3 rows of stereids. Upper laminal cells 12–16 µm wide, m long, with 1–4 papillae, each ± "c"– or "o"–shaped; upper marginal cells (9)12–16 µm wide, 9–12 µm long; transitional cells papillose almost to basal cells on abaxial surface, on adaxial surface smooth somewhat above basal cells; basal laminal cells 20–60 µm long, 9–18 µm wide, prominent, transverse walls dark-orange, longitudinal walls yellow or orange, superficial walls entire to irregularly ± perforated; basal marginal cells differentiated in 3–5 rows, yellowish. Goniautoicous. Perichaetial leaves oblong ad sheath-like below, broadly acute above and hair-pointed; perigonial leaves 1.0 mm long, sheath-like and acute or apiculate; perigonial paraphyses with upper cells entire, walls smooth.

Seta 4–7 mm long, erect to slightly curved, longitudinally ridged once or twice, almost untwisted; red. Capsule 1.5–2.5 mm long, when dry cylindric and furrowed, slightly constricted just below rim, slightly puckered at base and quickly contracted to seta, transluscent beige in furrows with red ribs and red rim; when old collapsed and deeply furrowed; exothecial cells in slightly irregular longitudinal rows, in transverse section groups of outer cells are heavily, evenly cutinized (form ribs of capsule), interspersed h groups of cells lightly, evenly cutinized; rim cells in 2 rows, opaque, dark-red, 14–20 µm wide, 7–16 µm long; walls thin; stomata superficial, restricted to capsule base, 30–53 µm long. Peristome in 1 concentric layer, teeth 16, lanceolate and slightly irregular, dark-red, outer surface ± strongly papillose, with 1 vertical row of cell plates, inner surface ± strongly papillose, with 2 vertical rows of cell plates; preperistome present. Annulus undifferentiated. Operculum 1.0 mm long, convex-rostrate. Spores brown, heteropolar, in polar view, 35–37 µm on equatorial axis, 20 µm X 35–37 µm on polar axis, proximal face ± smooth or sparsely papillose centrally, papillae solid, and ridged radially towards equator, distal face with prominent, warty protuberances, inner wall visible in most populations, entire surface irregularly papillose, papillae minute or surface appears irregular and vaguely roughened. Calyptra (2.0)2.7–5.0 mm long, extends well below capsule, narrowly elliptic–cylindric, distinctly narrowed to curved rostrum that is 1.0–1.2 mm long, cylinder with slight horizontal extension basally above well–defined fringe, segments broad, trapezoidal, calyptra golden–brown to dark–brown, dark–brown distally, with pale fringe, shiny, opaque, ± papillose to smooth; in transverse section cylinder with 2–3 rows of thick walls cells, fringe with 1 row thick walled cells; in superficial view fringe cells rectangular or irregularly elongate. Chromosome number unknown.

Habitat: Encalypta vittiana has been found in alpine tundra on limestone and dolomite outcrops, or on the lip of solifluction lobes. It occurs on small patches of otherwise base soil, or mixed in among other species of bryophytes and vascular plants. The microhabitat is always a protected one. Encalypta vittiana is invariably associated with substrates that are highly calcareous. At all of the localities where it has been found, E. vittiana occurs in mesic tundra on north, east or west–facing slopes. Some of the species characteristically associated with E. vittiana indicate the slightly mesic nature of the flora. Such species are Distichium inclinatum (Hedw.) B.S.G., Encalypta longicolla, Myurella julacea (Schwaegr.) B.S.G., Orthothecium intricatum (C. J. Hartm.) B.S.G. and O. strictum Lor. Other associates which have broader moisture tolerances include Bryoerythrophyllum recurvirostrum (Hedw.) Chen, Distichium capillaceum (Hedw.) B.S.G., Ditrichum flexicaule (Schwaegr.) Hampe and Tortella tortuosa (Hedw.) Limpr. The vascular plants most commonly associated with E. vittiana are Dryas integrifolia M. Vahl and Saxifraga oppositifolia L.

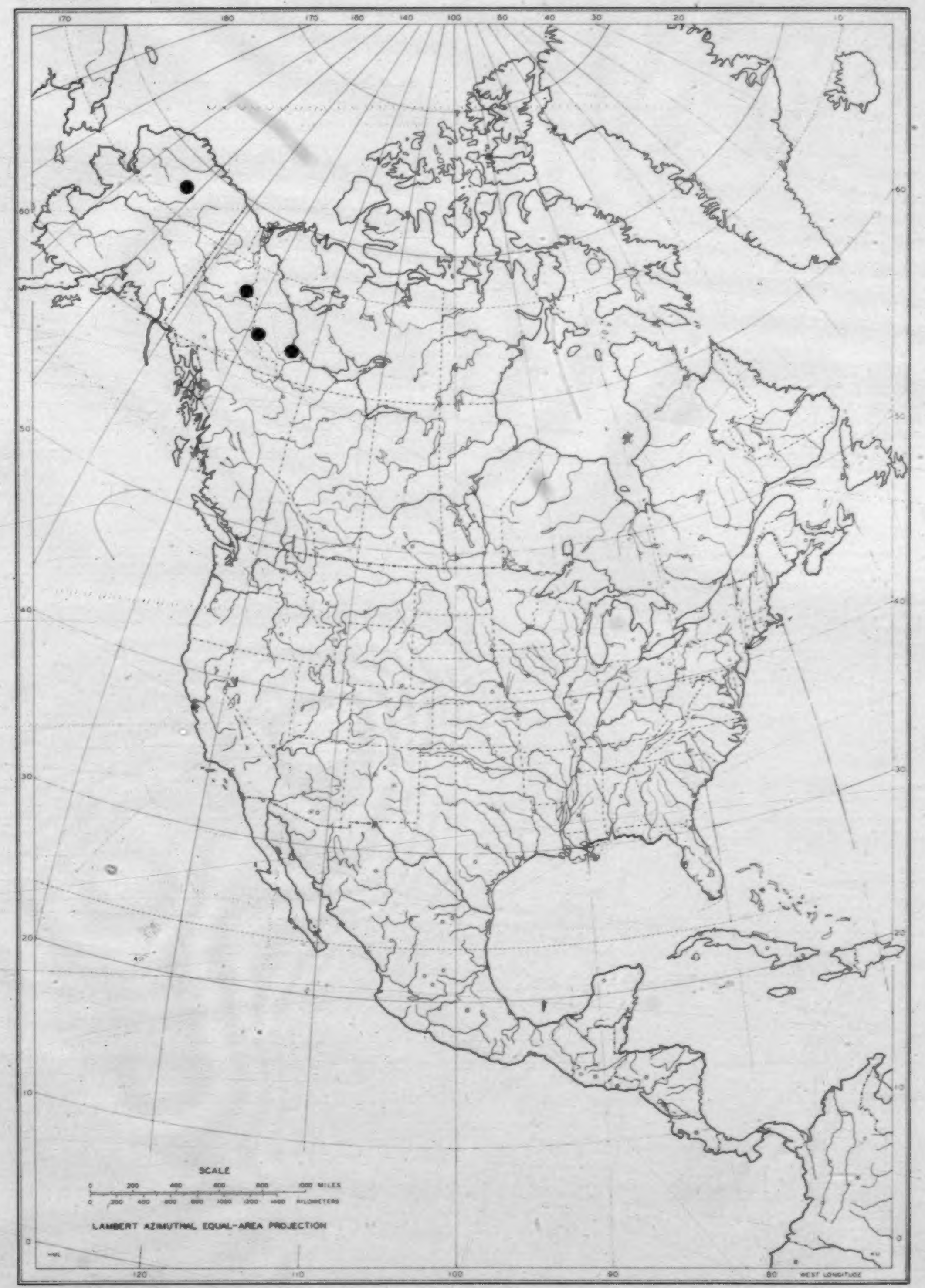
Distribution: Encalypta vittiana is known from two localities in the Brooks Range of Alaska, the Bonnet Plume Range in central–eastern Yukon Territory, the Logan Mountains in central–western Mackenzie District and the Nahanni Range in southwestern Mackenzie District of the Northwest Territories (Fig. 249).

Encalypta vittiana is presently known only from northwestern North America, where it is associated with the Western Cordillera within or near the regions of Alaska–Yukon that escaped glaciation in the Pleistocene (referred to as Beringia by Hultén 1937). The occurrence of species in this area, and in some outlying areas

Figure 249. Distribution of *Encalypta vittiana*.

NORTH AMERICA

No. 2


SCALE
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0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
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along the Cordillera farther south, has been described by Schofield (1969) as typical for endemic or circumpolar arctic-alpine bryophytes in North America. The species most closely related to these arctic-alpine taxa may occur nearby in circumboreal regions, or they may be more-or-less widely disjunct (Schofield 1969). Populations of *E. rhaptocarpa*, which is most closely related to *E. vittiana*, are concentrated along the western Cordillera north of the maximum extent of Wisconsin glaciation, and also occur in scattered localities across the boreal regions of North America. *Encalypta rhaptocarpa* should probably be considered an arctic-alpine, circumboreal moss, the range of which overlaps in northern regions with that of *E. vittiana*. Three arctic-alpine mosses with North American distributions similar to that of *E. vittiana* are *Andreaeobryum macrosporum* Steere and B. M. Murray (map in Steere 1978), *E. longicolla* and *Seligeria subimmersa* Lindb. (map in Vitt 1976). It is noteworthy that all three have been found at or near most of the localities where *E. vittiana* is reported from (*S. subimmersa* is now known from one of the Northwest Territories localities for *E. vittiana*; specimen in ALTA). These species, like *E. vittiana*, are restricted to substrates of a highly calcareous nature. However, the distributional restriction of these species cannot be attributed entirely to lack of suitable habitats. *Encalypta mutica* is similarly restricted to highly calcareous substrates, yet it is of much more frequent occurrence in northwestern North America than either *E. vittiana* or *E. longicolla*. The decimation of formerly more widely distributed populations by the Pleistocene glaciers, as suggested by Hultén (1937) and others (e.g. Packer & Vitt 1974) is a feasible explanation for the present narrow ranges of some of these species, while others may never have been more widespread. *Encalypta longicolla* and *S. subimmersa* are both known from Eurasia, as well as North America. It remains to be seen if *A. macrosporum* and *E. vittiana* will be reported from Eurasia in the future, or if they are both truly endemic elements of the North American arctic-alpine bryoflora.

Phylogenetic Relationships: The distinctive, warty protuberances on the distal surface of spores of *E. vittiana* establish that it belongs to the *E. rhaptocarpa-E. vulgaris* complex. As noted under Diagnosis and Differentiation, *E. vittiana* is most closely related to *E. rhaptocarpa*. The two species are indistinguishable on the basis of all structural features except the calyptra (see Diagnosis and Differentiation).

Specimens Examined: ALTA (3), CANM (1), Priv. Herb. D. G. Horton (2), NY (2).

ENCALYPTA SPATHULATA C. Müller,

Syn. 1: 519. 1849.

Figs. 250–261.

Type: "Hispania in fissuris rupium calcar. montis Santa Maria dicti in Sierra de Chiva. 5500' altitud. 2. Juni 1844: Wilkomm." (Lectotype: "Encalypta rhaptocarpa B pilifera Fk. In fissuris rupium calcareo. montis Sta Maria dicti Sierra de Chiva (c. 5500') 2. Juni 1844." G-Schwaegr.!; Isotypes: BM-Hampe!, G-DC!, H-Sol!, LAU-Colomb-Duplan!).

Leersia spathulata (C. Müll.) Lindb., Musci Scand. 20. 1879. *Nom. inval.*

Encalypta rhaptocarpa Schwaegr. var. *spathulata* (C. Müll.) Husn., Musc. Gall.: 198. 1887.

Encalypta extinctoria Swartz subsp. *tenella* Kindb. *in* Röll, Hedwigia 1896: 65. 1896. Type: "Rocky Mount.: Helena, Mont. Unter No. 1275 als Encal. vulgaris Hedw." (Lectotype: "N. Amer., 11/5 88 Montana, Helena J. Röll. Encalypta exstinctoria Sw. x E. tenella Kindb., n. subsp." S-Kindb.!).

Encalypta rhaptocarpa Schwaegr. subsp. *spathulata* (C. Müll.) Amann, Flore Mousses Suisse: 104. 1919.

Nomenclatural Notes: As discussed in Horton (1979c), *E. subspathulata* C. Müll. *et* Kindb. was described in 1892 (Macoun & Kindberg 1892) from a specimen that was probably part of the same collection that Macoun had earlier distributed as Canadian Musci No. 421, *E. spathulata*. While some of the exsiccata specimens consist of *E. spathulata*, at least in part, the lectotype in Kindberg's herbarium (S!) contains only plants that are a form of *E. rhaptocarpa*. Therefore, *E. subspathulata* is considered to be synonymous with the latter, not with *E. spathulata*. For further details, see Horton (1979c).

Diagnosis and Differentiation: *Encalypta spathulata* may well prove to be one of the most difficult species of *Encalypta* to differentiate because of variation in taxonomically critical character-states and convergence with another notoriously variable taxon, *E. rhaptocarpa*. However, there are some fairly reliable features that characterize most populations of *E. spathulata*. The most striking of these is that the plants, which generally occur in an extensive mat, are covered with a mass of pale-colored calyptrae. It is the very pale-golden color of the calyptra and the fact that it is transluscent, almost to the point of being transparent, that gives populations a very distinctive appearance. The rostrum of the calyptra is always short and clearly defined. Capsules are gymnostomous (a fragile, vestigial peristome has been observed only in a few populations from Montana) with a slight, but distinct, constriction just below the mouth and delicate, longitudinal plicae. The red to dark-red seta is quite fragile and many break when handled with forceps. Leaves are narrow and irregularly twisted, with a shiny costa that is a rich, dark-brown in many populations. Overall, the plants are very small. Microscopic features of *E. spathulata* include the clearly defined, marginal border at the base of the leaves and the prominent basal cells with orange transverse and yellowish longitudinal walls. The spores are heteropolar with large, verrucate protuberances on the distal surface and narrow, radial plicae on the proximal. Under the light microscope, the verrucae are hollow and an inner wall tracing the shape of the outer is generally visible.

Encalypta spathulata might be most readily confused with *E. flowersiana*, *E. mutica* or with some modifications of either *E. rhaptocarpa* or *E. vulgaris*. There are two, easily discernible features that differentiate *E. flowersiana*. The leaves are muticous and the distal surface of the spores is characterized by elongate, vermiform protuberances, in contrast to the discrete, verrucate ones of *E. spathulata*. Otherwise, these two closely related species are virtually identical.

Encalypta mutica resembles *E. spathulata* in the shiny, transluscent calyptra with a short, distinctly defined rostrum, the lack of a peristome and the small size of the plants. However, in *E. mutica* there is a distinct constriction at the base of the calyptra above a very precisely segmented fringe. While a more-or-less clearly defined fringe does occur in some populations of *E. spathulata* (see Variation), there is no constriction above it or only a very slight one. Leaves of *E. mutica* are always muticous and there is no

Figures 250-254. Encalypta spathulata. Scale=1 mm.

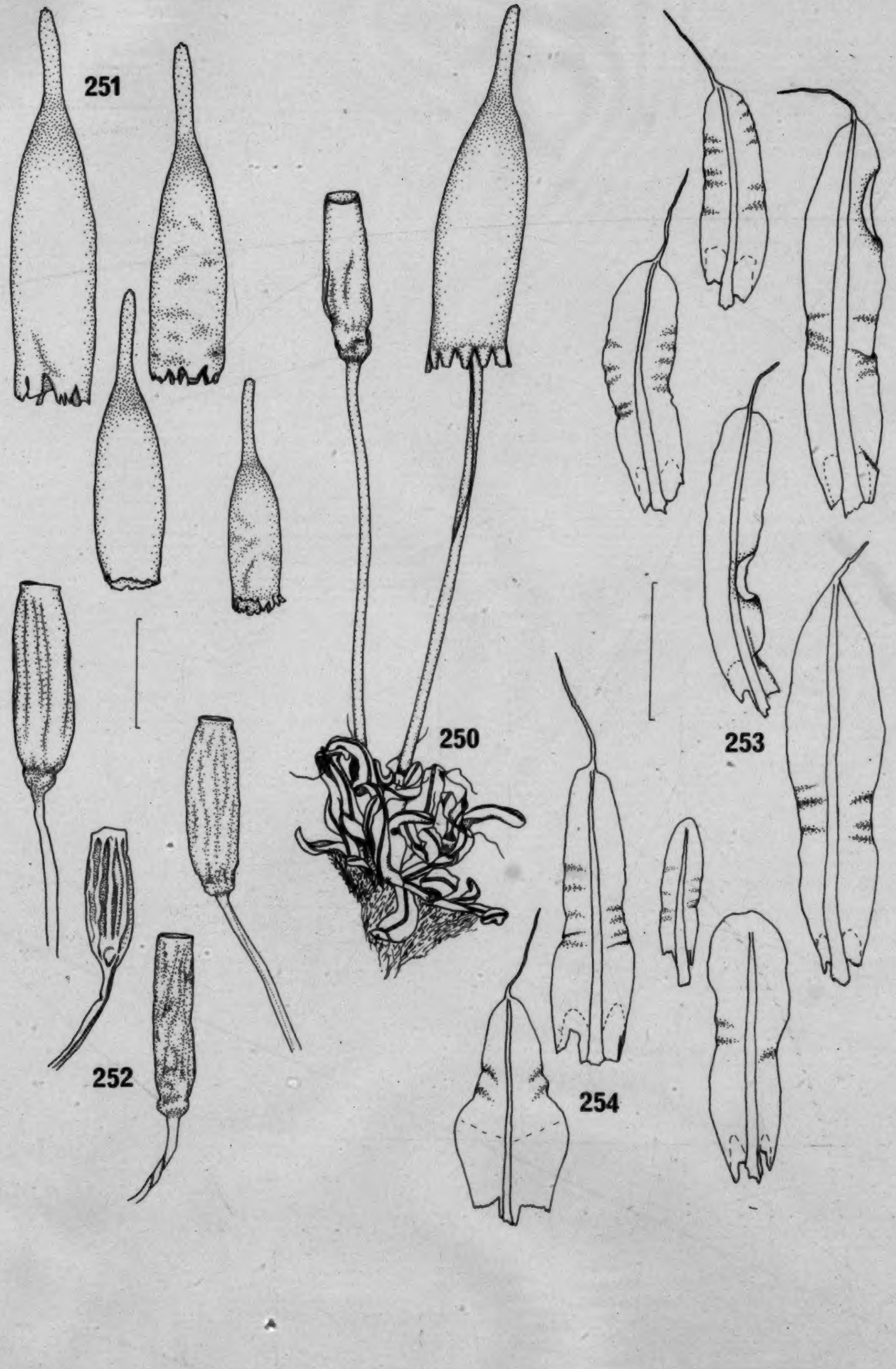
Fig. 250. Habit.

Fig. 251. Calyptrae.

Fig. 252. Capsules.

Fig. 253. Vegetative leaves.

Fig. 254. Perichaetial leaves.



Figures 255-258. *Encalypta spathulata* Spores.

Figs. 255 & 257. Distal surface.

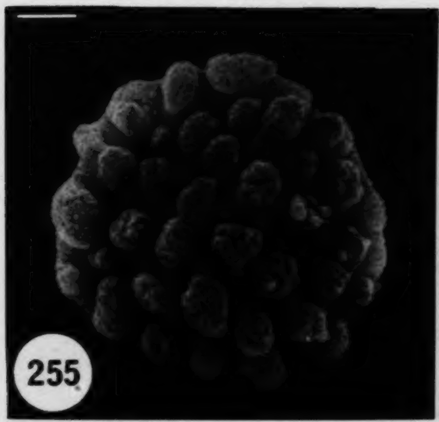
Fig. 255. Scale=5 μm.

Fig. 257. Scale=2 μm.

Figs. 256 & 258. Proximal surface.

Fig. 256. Scale=5 μm.

Fig. 258. Scale=2 μm.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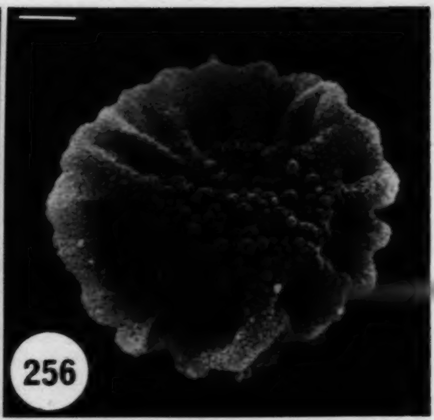
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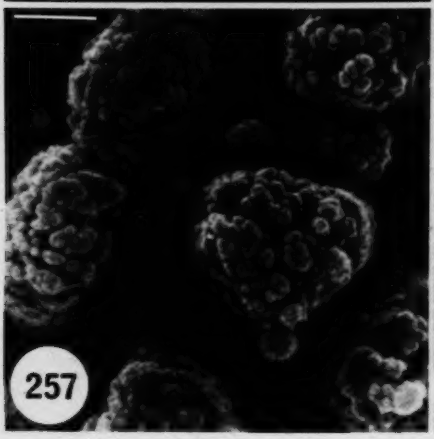
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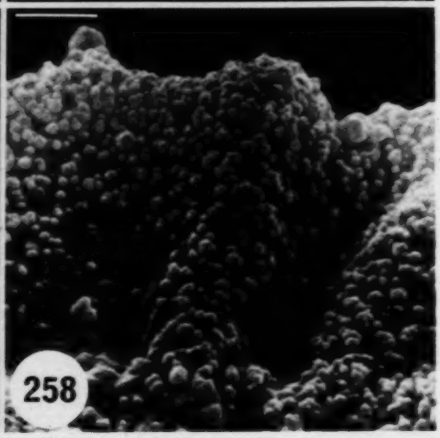

258

marginal border along the basal cells. The spores are paraisopolar and covered with small, gemmate protuberances.

Most species of *Encalypta* can be differentiated solely on the basis of spore structure; however, *E. spathulata* is one of a number of encalyptaceous taxa that are characterized by polar spores with large, warty protuberances on the distal surface. Such taxa are generally referred to *E. rhaptocarpa* or *E. vulgaris*, or subspecific categories of these two species. While *E. rhaptocarpa s. str.* and *E. vulgaris s. str.* are quite distinct, some of the myriad modifications of these two species approach *E. spathulata* quite closely. In fact, a number of the specimens determined as *E. spathulata* actually represent such modifications. For example, Limpricht's (1890) erroneous report of *E. spathulata* from Tirol is based upon such a specimen. *Encalypta rhaptocarpa s. str.* can be differentiated from *E. spathulata* by the opaque, golden calyptra, a well-developed, dark-orange peristome and capsules with dark-red, longitudinal ribs. *Encalypta vulgaris s. str.* is best differentiated by the muticous leaves with a prominent, shiny and golden-brown costa. The character-states that differentiate the modifications of these two species from *E. spathulata* are more subtle. Many populations of *E. spathulata* have the calyptrae distinctly fringed; this feature does not occur in *E. rhaptocarpa-E. vulgaris s. lat.* Also, the transluscency and very pale coloration of the calyptra of *E. spathulata* are particularly important features. In most instances, modifications of *E. rhaptocarpa-E. vulgaris* have a darker colored and more opaque calyptra. Capsules of *E. rhaptocarpa-E. vulgaris s. lat.* generally lack the slight constriction just below the mouth, leaves tend to be broader and plants tend to be larger than those of *E. spathulata*.

Description: *Plants* to 8 mm tall, olive-green to light-green above in most populations, glaucous-green in few, brown below, ± branched. *Stem* in transverse section with central strand undifferentiated or ± distinct, cells small, walls thin and hyaline. *Brood bodies* absent. *Axillary hairs* sparse. *Leaves* when dry incurved and irregularly ± twisted, laminae conduplicate to inflexed; (1.3)1.7–3.0(4.0) mm long, (0.2)0.3–0.6(1.1) mm wide, oblong-ligulate to narrowly oblong or narrowly spathulate, apex abruptly narrowed, gradually narrowed in some, to hair-point that is ≤1.5 mm long, lower leaves shorter, ligulate to spathulate, muticous; *margins* plane, minutely irregular in outline near apex.

Costa excurrent, ends well below apex in lower leaves, abaxial surface prominently keeled, very shiny to moderately shiny, golden-brown to dark-brown, transluscent-green on young leaves, smooth below, sparsely papillose in few populations, sparsely papillose distally; in transverse section 2-3 rows ventral cells, begleiters undifferentiated, 2-3 rows stereids. Upper laminal cells (7)12-15(20) μm wide, (9)12-18(23) μm long, with 2-3(4) papillae per cell, each ± distinctly "c"-shaped, few "o"-shaped; upper marginal cells 12-15(17) μm wide, 9-15 μm long; transitional cells papillose to basal cells on abaxial surface, on adaxial surface walls smooth somewhat above basal cells; basal laminal cells (17)26-70(87) μm long, 12-20(26) μm wide, prominent, transverse walls orange, longitudinal walls yellowish, superficial walls smooth, entire to irregularly ± perforated; basal marginal cells distinctly differentiated in rows. Goniautoicous. Perichaetial leaves ± broadly ovate and sheath-like below, oblong above; perigonial leaves 0.8-1.2 mm long, ± broadly oblong and sheath-like, abruptly narrowed, apex muticous to hair-pointed; perigonial paraphyses with some upper cells longitudinally divided, walls smooth or with 1-3 low, rounded papillae distally.

Seta (2)3-6(8) mm long, erect to flexuose, slightly twisted sinistrorsely below, laxly twisted dextrorsely near capsule, shiny and red to dark-red; in transverse section 145-160 μm in diameter. Capsule (1.0)1.3-2.1(2.3) mm long, when dry cylindric to elliptic-cylindric, delicately striate, plicate or delicately ribbed, ± constricted beneath rim, puckered basally and abruptly contracted to seta, golden with narrow red rim and faint golden-brown to relatively distinct red-brown, longitudinal ribs; when old dull-brown and ± collapsed; exothecial cells 60-165μm long, 9-29μm wide, in ± regular, longitudinal rows, in transverse section intermittent groups of 1-5 cells with walls thickened, 5μm thick, other cells with walls thin; rim cells in 1-2 irregular rows, 12-20μm wide, 6 -17μm long, walls thin; stomata superficial, restricted to capsule base, 40-44 μm long. Peristome absent in most populations, few with 1 concentric layer, teeth 16, hyaline or white, ± truncate, outer surface with 1 vertical row of cell plates, sparsely papillose, inner surface with 2 vertical rows of cell plates at base, smooth; preperistome absent. Operculum 0.6 mm long, convex-rostrate. Annulus undifferentiated. Spores brown, heteropolar, in polar view radially symmetric and circular, 29-35 μm, in equatorial view polarly asymmetric and concave-convex, 29-35 μm X 20-23 μm, proximal face ±

smooth centrally or with low gemmae, radially plicate; distal face with prominent, warty protuberances; deposition of microgranules over entire surface. *Calyptra* 2.0–4.0 mm long, narrowly elliptic–cylindric and distinctly contracted to slightly curved or erect rostrum that is (0.6)0.8–1.0 mm long, at base some slightly constricted above short fringe, some irregularly, shortly lacerate, some erose, calyptra golden to pale–golden, some brown distally, shiny and transluscent; in transverse section cylinder with 2–3 layers of cells with very thick walls, fringe with 1 row of cells, walls strongly thickened; in superficial view fringe cells short–oblong to quadrate. *Chromosome number* unreported.

Habitat: Quite clearly, *E. spathulata* is restricted to highly calcareous substrates. In North America, the underlying substrate where populations have been collected is typically limestone. The pH of soil samples taken with many of these populations ranged from 7.0 to 7.7 (n=23 from 13 different localities) with a mean of 7.4 (s.d.=±0.2) (Fig. 300). The concentrations of Ca^{++} and Mg^{++} recorded from some of these same soil samples were also relatively high (Figs. 301–302, Table 9). Similarly, the habitat data on the European specimens invariably refer to a calcareous substrate. This is particularly noteworthy considering that the European localities are strikingly widespread by comparison to those in North America.

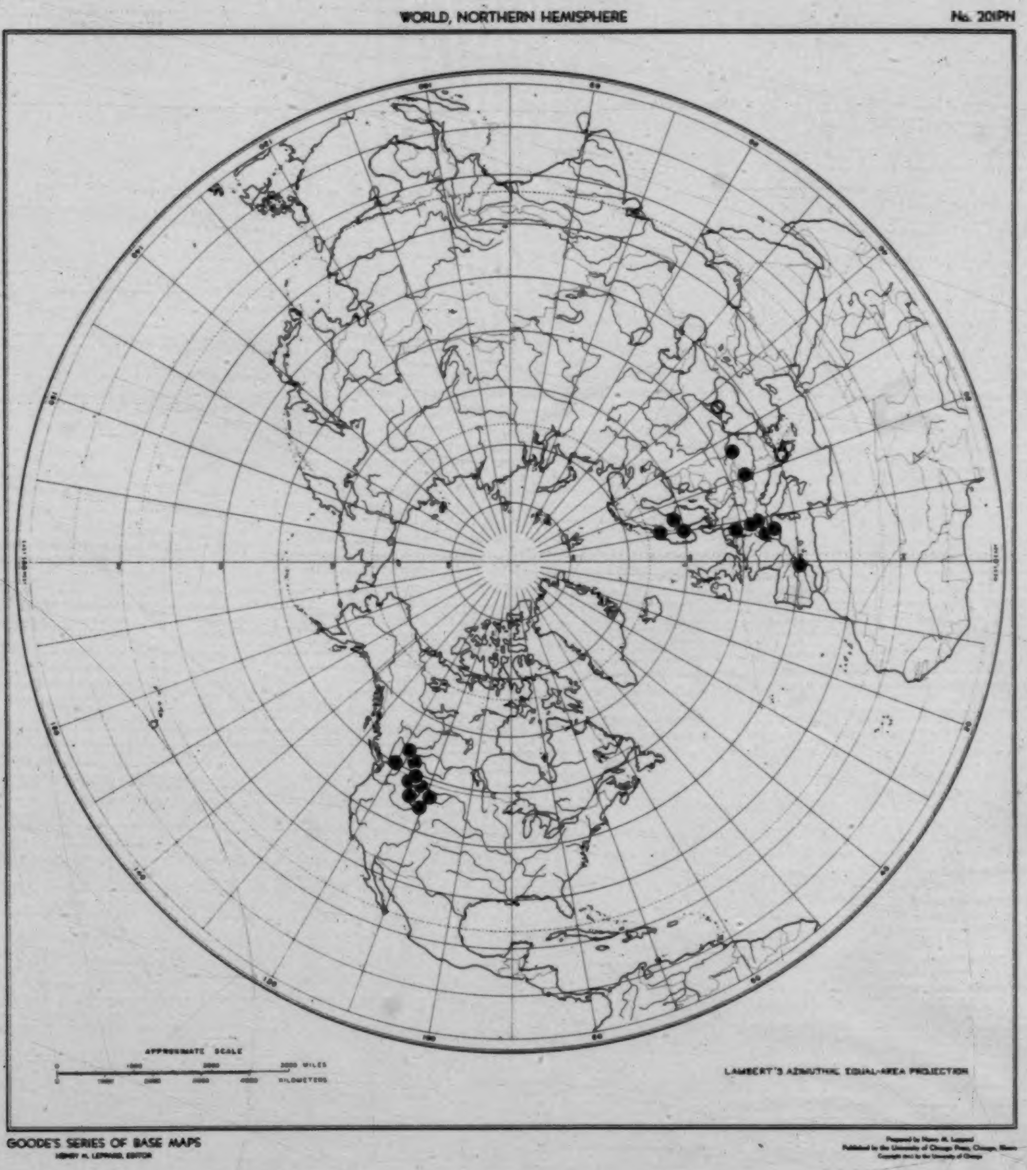
Populations of *E. spathulata* occur at lower elevations in montane or hilly terrain. In North America, they have been found at elevations of 1025 to 1770 metres, while the European collections are from 150 to 1700 metres. In North America, *E. spathulata* grows on patches of bare, moist soil in such shaded habitats as *Picea glauca–Populus tremuloides* and *Pseudotsuga menziesii* forests, montane *Pinus contorta–Picea glauca* or subalpine *Abies lasiocarpa–Picea engelmannii* forests. Apparently, this species does not occur in tundra habitats in either North America or Europe. *Encalypta spathulata* grows on rock outcrops, as is characteristic of most species of *Encalypta*; however, populations are more extensive and common in such ruderal and disturbed habitats as roadside banks or in the hollow created by an uprooted tree. The "weediness" of this habitat is reflected in such common associates as *Barbula convoluta* Hedw., *Bryoerythrophyllum recurvirostrum* (Hedw.) Chen, *Bryum* spp., *Ceratodon purpureus* (Hedw.) Brid. and *Tortula* *mucronifolia* Schwaegr. *Encalypta spathulata* may have rather limited tolerance of moisture stress. In the southern Canadian Rockies some populations of *E. mutica* occur in similar habitats to those of *E. spathulata* and populations of the two species are not uncommonly found intermixed. However, *E. mutica* seems to have a broader range of tolerance as it also occurs in more exposed and drier habitats.

Distribution: *Encalypta spathulata* is known from North America, northern, central and southern Europe (Fig. 259), and it has also been reported from southeastern Europe and central Asia (Savicz-Ljubitskaja & Smirnova 1970). In North America, it has been reported from Alberta in the Rocky Mountains; from British Columbia in the Rocky Mountains and slightly disjunct in the northern Cascade Range; from Montana in the Rockies, and just east in the Great Falls area and the Big Snowy Mountains (Horton 1979c) (Fig. 260). See Horton (1979c) and Horton (1981a) for discussions of the phytogeographical significance of the North American distribution of *E. spathulata*.

In Europe, *E. spathulata* is reported from Norway in Nord-Tröndelag and Buskerud; from Sweden in Dalarna; from Spain in Valencia; from France in Haute Savoie and Alpes Maritimes; from West Germany in North Rhine-Westphalia and Baden-Wurttemberg; from Switzerland in Graubünden; from Austria in Styria; and from Romania in Brasov (Fig. 261). Kuc (1973b) also reported *E. spathulata* from Svalbard (indicated on Fig. with an open circle), Nyholm (1954) included Finland, and Savicz-Ljubitskaja and Smirnova (1970) reported it from Kavkaz (indicated on Figs. 259, 261 with an open circle) and the Ukraine. I have not been able to trace a specimen of *E. spathulata* from Finland and I am unable to confirm the other reports because the requested specimens have not been made available to me for study. Müller (1901) cited a specimen of *E. spathulata* from the peak of Karava in the Pindus Mountains of Greece, which he stated had been collected by Haussknecht in 1885. Unfortunately, it is not possible to verify this report, although *E. spathulata* may well occur in this region, because I have not been able to find the specimen in Haussknecht's herbarium in JE. Savicz-Ljubitskaja and Smirnova (1970) also reported *E. spathulata* from central Asia.

Encalypta spathulata is very rare, but the populations are characteristically extensive. In North America, it is known from quite a number of different localities within

Figure 259. Distribution of *Encalypta spathulata*.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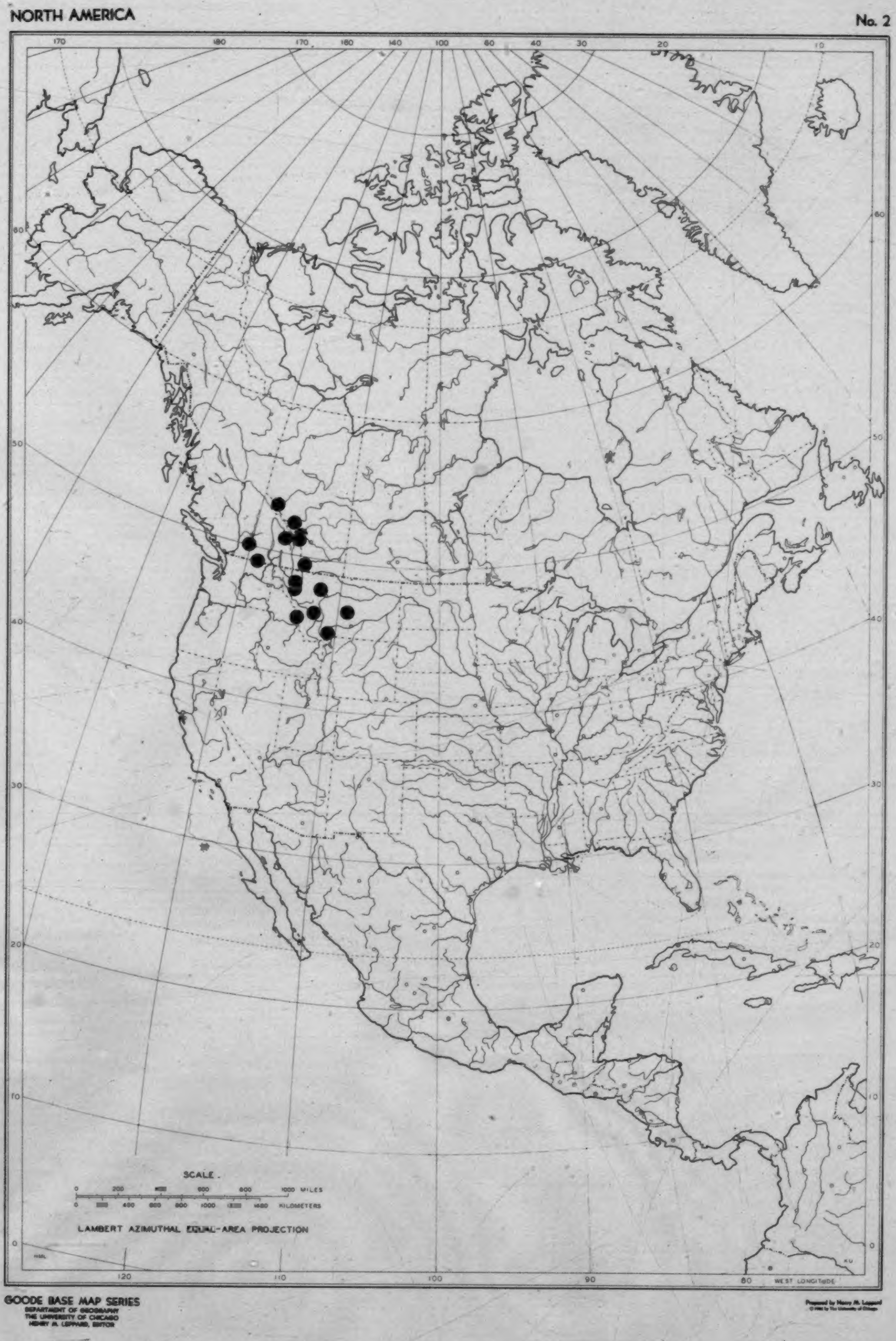
No. 201PN
APPROXIMATE SCALE
0
1000
2000
3000 MILES
0
1000
2000
3000
4000
KILOMETERS
LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION
GOODE'S SERIES OF BASE MAPS
HENRY M. LEPPARD, EDITOR
Prepared by Henry M. Leppard
Published by the University of Chicago Press, Chicago, Illinois

Figure 260. Distribution of Encalypta spathulata in North America.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No. 2
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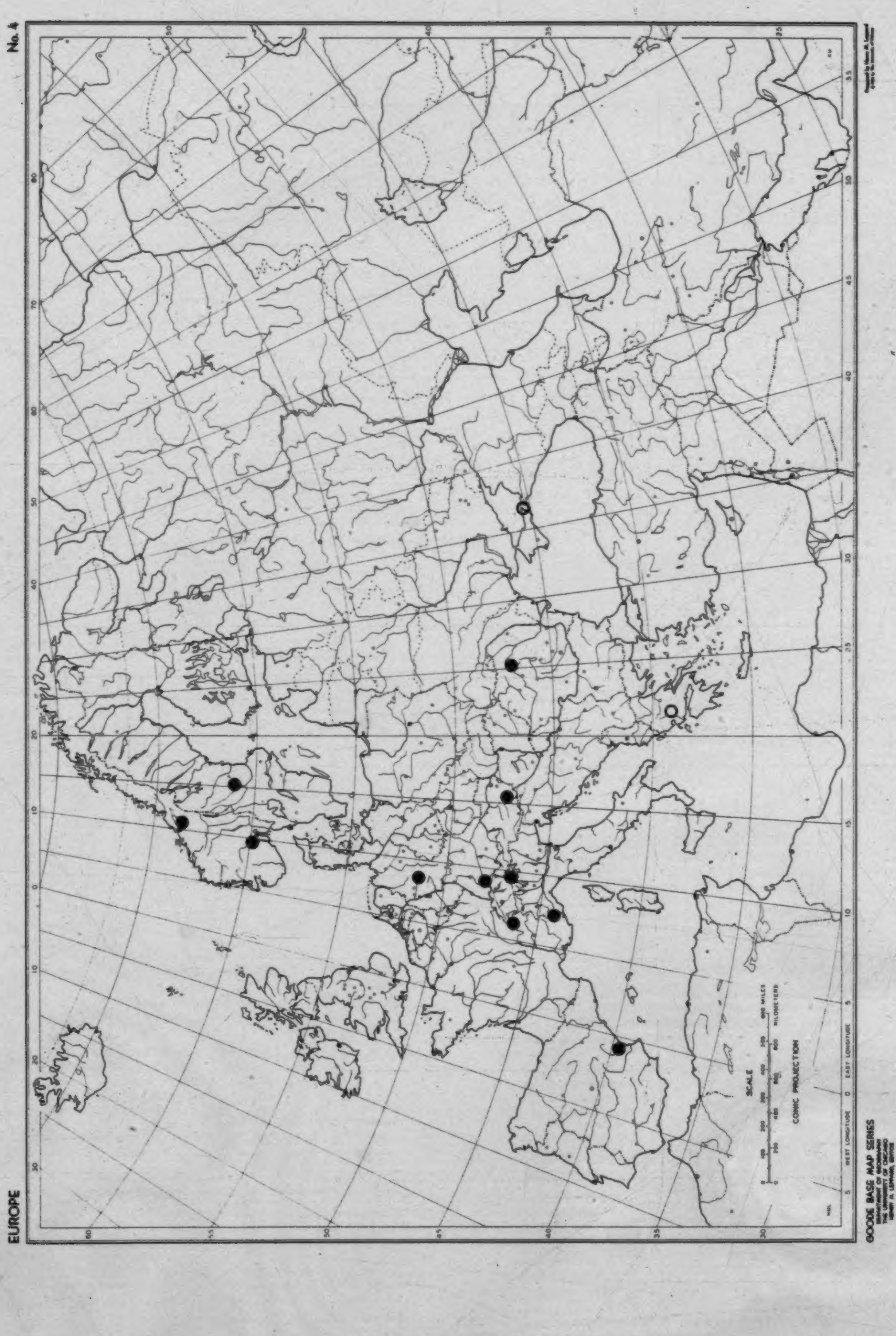
0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
WEST LONGITUDE
120
110
100
90
80
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR
Prepared by Henry M. Leppard

Figure 261. Distribution of *Encalypta spathulata* in Europe.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SCALE
100 200 300 400 500 600 MILES
200 400 600 800 KILOMETERS
CONIC PROJECTION
WEST LONGITUDE
EAST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

a very limited range. While populations from Montana, Alberta and British Columbia have been in mats larger enough for distribution in exsiccatae (Horton 1979a), it can not be considered common. In Europe, the localities that E. spathulata is reported from are contrastingly widespread, but these reports are based upon only one or two collections in each instance. Apparently the populations were also extensive as two are contained in exsiccatae (Bauer's Musci europaei exsiccati No. 844 and Rabenhorst's Bryotheca europaea No. 1163) and several others, including the type, are represented by numerous duplicates.

Variation: (1) There is remarkable interpopulational variation in structure of calyptrae and capsules of E. spathulata. The type specimens of E. spathulata are characterized by a somewhat irregular fringe at the base of the calyptra (as in Fig. 251, upper right). Calyptrae from different populations are erose and partially fringed or almost entire at the base (Fig. 251, lower left); occasionally, the fringe is well-defined as in the habit illustrated (Fig. 250). The rostrum of the calyptra varies little in length (Figs. 250–251), but may be quite narrow (Fig. 251 – lower right) to relatively broad (Fig. 251, upper). Calyptrae with a thicker rostrum are readily confused with those of E. rhaptocarpa, particularly if a fringe is not present. Mature capsules are generally constricted beneath the rim and narrowly elliptic-cylindric (Fig. 252 – upper left and right); however, it is not uncommon for populations to lack this constriction and to be cylindric in shape (Fig. 252 –lower). The capsules are irregularly wrinkled, evenly and delicately striate, unevenly striate or furrowed with rather well-defined ribs (Fig. 252). In this latter situation, the capsules approach those of 'typical' E. rhaptocarpa. This variability in some of the critical character-states makes it difficult to define E. spathulata structurally, particularly in relation to the closely related taxa of the E. rhaptocarpa-E. vulgaris complex, but does not negate the validity of recognizing this taxon at the specific level.

(2) A collection of E. spathulata from Montana (Horton 12967 – ALTA) consists of some plants with leaves in which some or all of the upper laminal cells are more-or-less smooth (for a more complete description and illustrations, see Horton (1978)). While this parallels the condition of the upper leaf cells of Bryobrittonia, it is considered to be an isolated occurrence that has no reflection on the generic status of Encalypta and

Bryobrittonia (see discussion under Conspectus of Genera of Encalyptaceae).

Phylogenetic Relationships: The "warty" spores of *E. spathulata* indicate that it is allied to the *E. rhaptocarpa*–*E. vulgaris* complex. *Encalypta spathulata* is most closely related to *E. flowersiana* (see Phylogenetic Relationships of *E. flowersiana*) and to *E. rhaptocarpa*. *Encalypta rhaptocarpa* parallels *E. spathulata* in the characteristics of plicate, more-or-less ribbed capsules, red seta and leaves with a long hair-pointed apex. Furthermore, the forms of *E. spathulata* with the calyptra more broadly rostrate and more-or-less erose at the base resemlbe *E. rhaptocarpa* even more closely.

Specimens Examined: ALA (2), ALTA(30), BP (7), FI (1), G-Hedw.-Schwaegr. (1), H-Sol (3), Priv. Herb. D. G. Horton (19), LAU (1), M (5), O (3), PC (2), S (12).

ENCALYPTA FLOWERSIANA Horton,

Bryologist 82: 374, figs. 12–23. 1979.

Figs. 262–271.

Types: "HAITI: DEPARTMENT DE L'OUEST: near summit of Pic La Selle, Morne La Selle, ca. 2675 m. Over limestone in open, burned-over pine forest with *Agave*, *Wetmore 3129* (Holotype – CANM; Isotype – MSC); *Imshaug 22999* (Paratype – CANM). GUATEMALA: DEPT. HUEHUETENANGO: along road in region of Chemal, Sierra de los Cuchumatanes, at km 36, alt. about 3300 m, *Standley 83090b* (Paratypes – F, FH-Bartram).".

Diagnosis and Differentiation: *Encalypta flowersiana* is differentiated from all other species of *Encalypta* by the prominent, vermiform protuberances on the distal surface of the polar spores. Other definitive features of *E. flowersiana* include the pale-golden, very transluscent calyptra with a short, narrow rostrum. Capsules are longitudinally striate or faintly plicate and there is no peristome. The red seta is short, and the narrow, muticous leaves are irregularly twisted when dry. Microscopically, there is a marginal border at the base of the leaves and the basal cells are prominent with orange transverse walls. Overall, the plants of E. flowersiana are tiny and some populations are extensive.

Encalypta flowersiana might be confused with some other taxa of the E. rhaptocarpa-E. vulgaris complex, particularly E. spathulata. Character-states of calyptrae and capsules, and the contorted habit of the leaves of E. flowersiana parallel those of E. spathulata. Populations of E. spathulata characteristically occur in extensive short-tufts and this also appears to be a feature of E. flowersiana as the holotype and isotype must have formed a rather extensive mat. Encalypta spathulata is differentiated from E. flowersiana by hair-pointed leaves. Warty, rounded protuberances on the distal surface of the spores differentiate not only E. spathulata, but also all other species in the E. rhaptocarpa-E. vulgaris complex.

Encalypta flowersiana is superficially similar to E. mutica in character-states of the calyptra, the gymnostomous capsules and muticous leaves. Encalypta mutica is best differentiated structurally by indistinctly polar spores with the entire surface covered more-or-less regularly by small gemmae. However, these two species are also segregated geographically, as E. mutica is presently known only from north of the Canada-United States boundary along the Western Cordillera.

Description: Plants to 11 mm tall, olive- to yellow-green above, brown below; ± branched. Stem in transverse section with central strand distinct, cells small, walls thin and hyaline. Brood bodies absent. Axillary hairs sparse. Leaves when dry incurved and irregularly twisted, laminae conduplicate to inflexed; 1.8-3.0 mm long, 0.5-0.9 mm wide, oblong, narrowly oblong, narrowly elliptic-oblong or narrowly lingulate, apex obtuse to broadly rounded and muticous, lower leaves smaller; margins plane. Costa subpercurrent, abaxial surface keeled, moderately shiny, transluscent-green to dark-brown, smooth below, sparsely papillose distally; in transverse section with 2-3 rows ventral cells, begleiters undifferentiated, 2-3 rows of stereids. Upper laminal cells 9-14 μm wide (7)9-16 μm long, (2)3-4 papillae per cells, ± distinctly "c"-shaped; upper marginal cells 9-12 μm wide, 7-12 μm long; transitional cells with papillae to basal cells on abaxial surface, on adaxial surface smooth somewhat above basal cells; basal laminal cells 25-50 μm long, 9-14 μm wide, prominent, transverse walls orange, longitudinal walls

Figures 262-266. **Encalypta flowersiana**. Scale=1 mm.

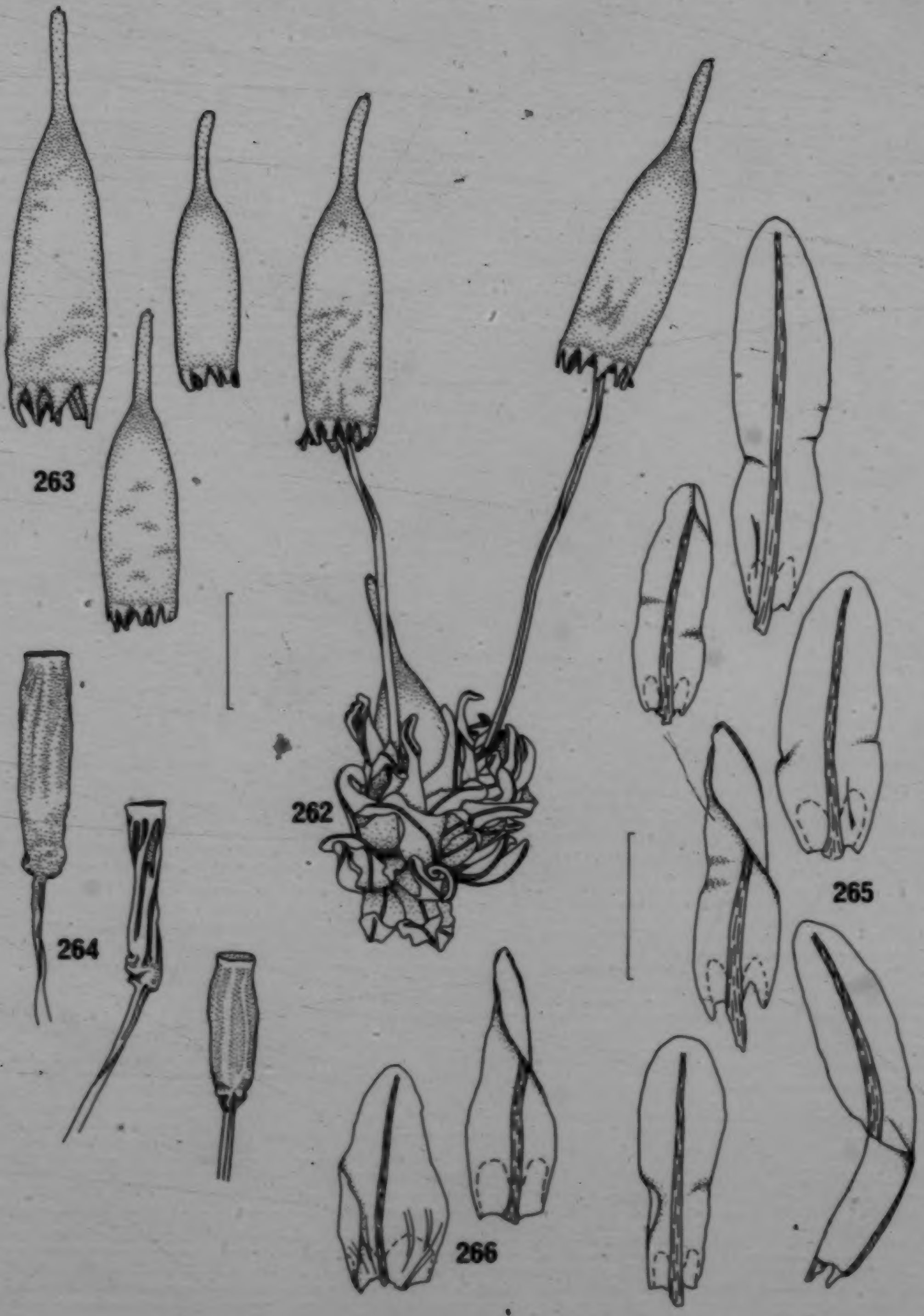
Fig. 262. Habit.

Fig. 263. Calyptrae.

Fig. 264. Capsules.

Fig. 265. Vegetative leaves.

Fig. 266. Perichaetial leaves.



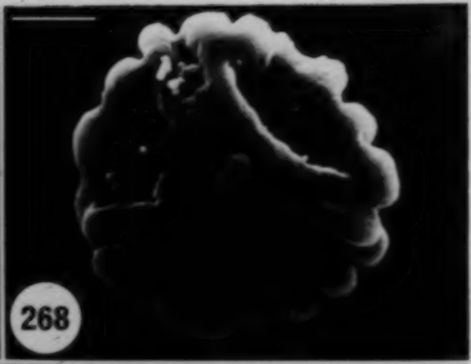
Figures 267-270. Encalypta flowersiana Spores. Scale=10 μm.

Fig. 267. Distal surface.

Fig. 268. Proximal surface.

Figs. 269-270. Distal surface.

267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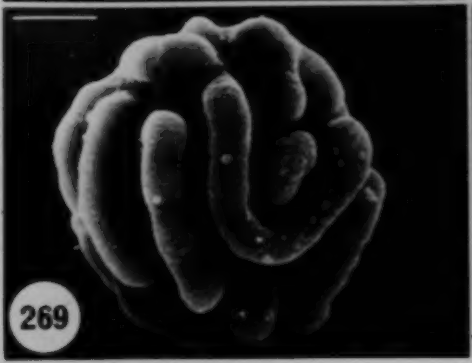
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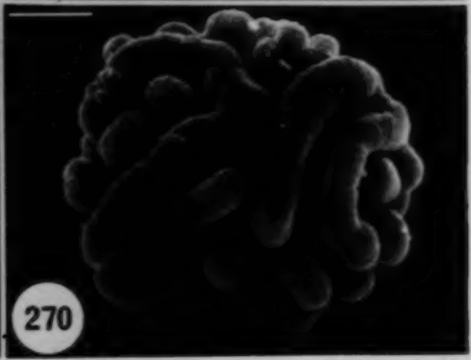

270

yellowish, superficial walls smooth, entire to irregularly ± perforated; basal marginal cells distinctly differentiated in rows. Goniautoicous. Perichaetial leaves ± sheath-like; perigonial leaves 0.8–1.2 mm long, sheath-like and ± broadly oblong, abruptly narrowed to broadly acute apex, muticous; perigonial paraphyses with upper cells entire, walls with 1–3 low, rounded papillae, some smooth.

Seta 3–5 mm long, erect to flexuose, untwisted to once-twisted dextrorsely near base of capsule, shiny and red; in transverse section 145–160 µm in diameter. Capsule 1.3–2.0 mm long, when dry short-cylindric, delicately striate to faintly plicate, slightly constricted just below rim, puckered basally and abruptly contracted to seta, pale-golden with pale-red rim and striations or plications golden to brownish; when old dull-brown and furrowed; exothecial cells 55–145 µm long, 9–23 µm wide, in ± regular, longitudinal rows, in transverse section intermittent groups of 1–5 cells with walls slightly thickened, 3 µm thick, other cells with walls thin; rim cells in 1–2 irregular rows, 18 µm wide, 5–16 µm long, walls thin; stomata superficial, restricted to capsule base, 35–41 µm long. Peristome absent. Operculum 0.7 mm long, convex-rostrate. Annulus undifferentiated. Spores brown, polar, in polar view radially symmetric and circular, 37–39 m, in equatorial view polarly asymmetric and concave-convex, 37–39 µm X 28 µm, proximal face with low gemmae centrally, radially plicate; distal exine with prominent, vermicular and warty protuberances; entire surface ± granular and pitted between protuberances. Calyptra 2.8–4.0 mm long, narrowly elliptic-cylindric and distinctly contracted to slightly curved or erect rostrum that is 0.8–1.0 mm long, cylinder slightly constricted basally above short fringe to irregularly, shortly lacerate, calyptra pale-golden to brown distally, shiny and transparent, smooth with few low, rounded papillae on rostrum; in transverse section cylinder with 2–3 layers of cells with very thick walls, fringe with 1 row of cells, walls strongly thickened; in superficial view fringe cells short-oblong to oblong. Chromosome number unreported.

Habitat When *E. flowersiana* was described (Horton 1979b), it was known from only two localities. As a result, the discussion of habitat contained rather tentative generalizations. Populations were reported to grow on soil in disturbed habitats at high elevations. However, based upon inferences drawn from the habitat-preferences of the closely related *E. spathulata* and information on the three presently known localities of *E. flowersiana*, it is possible to characterize the habitat of the latter species more accurately. Populations of *E. flowersiana* have been collected on soil in more-or-less forested habitats at elevations of 2200 to 3300 metres. Standley's Guatemalan collection is from a dense *Juniperus* forest and Magill's collections from Texas are from a *Pinus-Quercus-Juniperus* forest. Wetmore and Imshaug collected *E. flowersiana* in an open, burned-over *Pinus* forest with *Agave* ground cover. In the original publication (Horton 1979b), it was stressed that this species had been found at high elevations. While this is indeed true, such a statement might be mistakenly interpreted to indicate that *E. flowersiana* occurs in alpine tundra. It now seems probable that quite the opposite is the situation. As the collections of *E. flowersiana* are all from below treeline, and *E. spathulata* is one of the few species of *Encalypta* that is restricted to forested habitats (see Habitat under *E. spathulata*), it appears that *E. flowersiana* should be looked for in subtropical, montane regions below the upper elevational limit of trees.

The habitat of *E. flowersiana* was originally considered to be rather 'weedy' (Horton 1979b), that is, disturbed, irrespective of whether the disturbance is caused by man or natural forces. This conclusion was based upon such associated species as *Anoectangium aestivum* (Hedw.) Mitt., *Barbula convoluta* Hedw., *Distichium capillaceum* (Hedw.) B.S.G. and *Eurhynchium pulchellum* (Hedw.) Jenn., and the information that the holotype collection came from an area that had been burned several times. The suggestion that *E. flowersiana* grows in disturbed habitats is further supported by the species associated with the Texas populations, which include such 'weeds' as *Bryum argenteum* Hedw. and *B. billardieri* Schwaegr. *Encalypta spathulata* is similarly characteristic of such disturbed habitats as roadside ditches.

As with *E. spathulata*, it is probable that *E. flowersiana* is restricted to highly calcareous substrates. The holotype collection from Haiti was collected "...very near the actual summit" of Pic La Selle, which "...is a small point of dry limestone in an open area." (Wetmore *in litt.*). While the substrate in the Emory Peak area of the Chisos Mountains in Texas is largely igneous, there are also "...very small, isolated outcrops of soft chalk or lime." (Magill *in litt.*), so the collections of *E. flowersiana* may well have come from one of these. As noted in Horton (1979b), the occurrence of such other calciphiles as

Orthotrichum anomalum Hedw. in the Huehuetenango region of Guatemala (Vitt *pers. comm.*) indicates that calcareous substrates occur in the general area where *E. flowersiana* was collected.

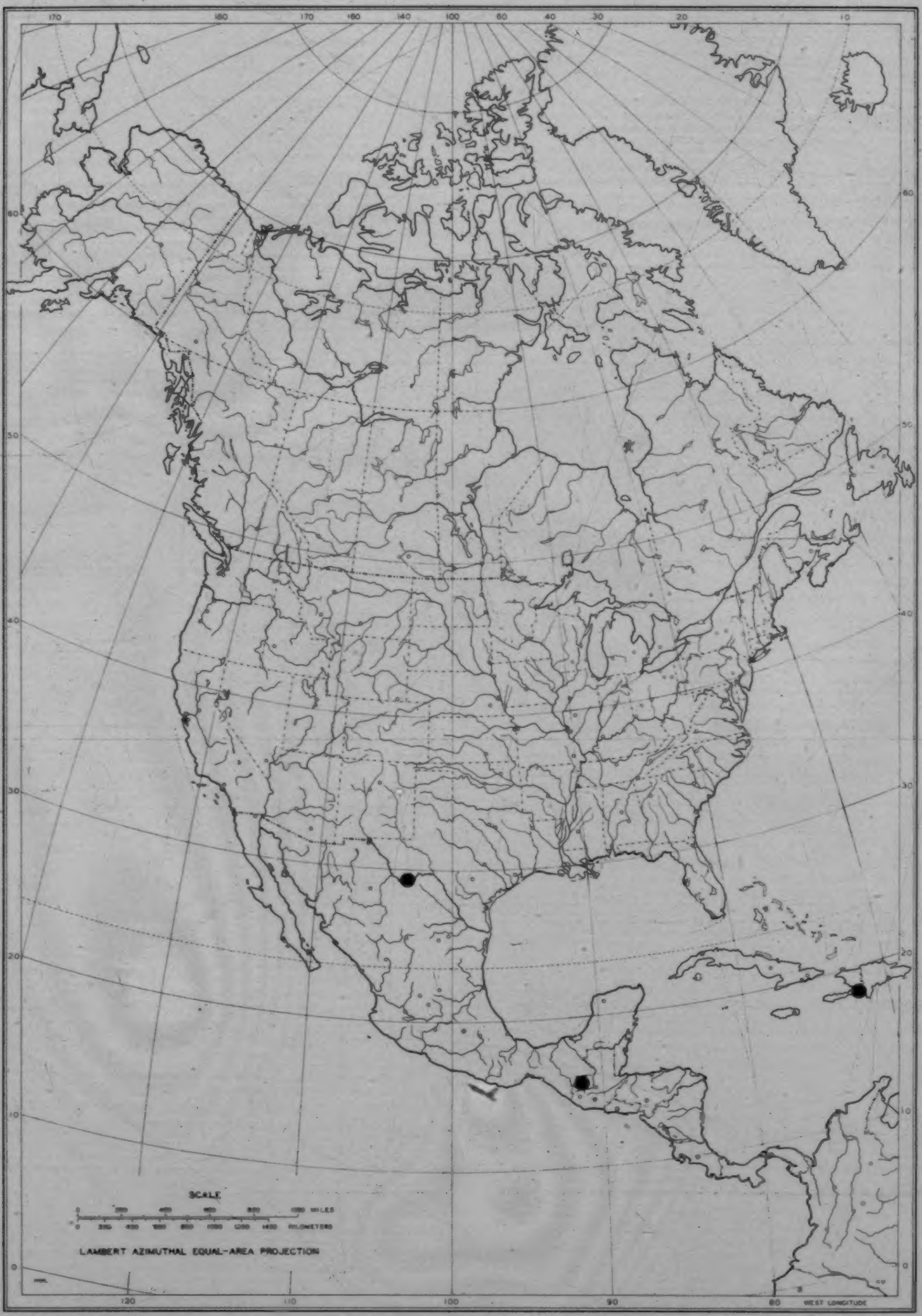
In more northerly areas of North America, particularly north of the maximum extent of Wisconsin glaciation along the Cordilleran axis, most species of *Encalypta*, as with other northern species of bryophytes, show less restriction with respect to differences in altitude than vascular plants (Lee & La Roi 1979). However, farther south, as in Mexico and Central America, where species richness of such northern genera is dramatically reduced, the "northern" species are restricted to tundra habitats. For example, populations of *E. ciliata* occur primarily in forested habitats but also in tundra in northwestern North America, but in tropical and subtropical regions they are restricted to the alpine zone. In contrast, *E. flowersiana* is not known from tundra habitats, although it appears to be restricted to montane regions. As this species is known from several relatively widespread localities, this indicates that dispersal of some species of *Encalypta* is effective in montane, forested habitats of subtropical regions. Therefore, ineffective dispersal is probably not the reason that such "northern" species of *Encalypta* as *E. ciliata* do not occur at lower elevations. Their restriction to alpine habitats may be a function of competition or reflect a lack of appropriate habitats at lower altitudes.

Distribution: *Encalypta flowersiana* is restricted to the New World. It is reported from southern North America in the Chisos Mountains of Texas, in Central America from the Sierra de los Cuchumatanes in Guatemala and in the Greater Antilles from Pic La Selle in Haiti (Fig. 271).

Encalypta flowersiana was described on the basis of collections from Guatemala and Haiti (Horton 1979b) and has been reported recently from the Texas locality (Horton 1980). In the original publication, it was suggested that *E. flowersiana* probably also occurs in the mountains of Chiapas, Mexico, but not in the Central Volcanic Highlands. While I would presently concur with both statements, it can be added that it is not be expected in the Central Volcanic Highlands because the substrate is not calcareous. *Encalypta flowersiana* should also be looked for in forested habitats on Cerro Potosi where the underlying rock is reported to limestone (Delgadillo 1971). The importance of

Figure 271. Distribution of Encalypta flowersiana.

NORTH AMERICA **No. 2**


SCALE
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LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
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WEST LONGITUDE
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10
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GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

Prepared by Henry M. Leppard
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looking for E. flowersiana in forested and not tundra habitats is stressed.

The structural similarities between E. flowersiana and E. spathulata are so striking as to suggest derivation of one taxon from the other. Furthermore, the distribution patterns of these two species, relative to one another, provide evidence that E. flowersiana evolved from E. spathulata as a result of geographic isolation. A species with a very restricted distribution may be considered to be either very old or very young. As E. spathulata is rather widespread in Europe and also occurs in North America, while E. flowersiana is restricted to localities in southern North America and Central America, it is more probable that E. flowersiana is the younger, more recently evolved species. In North America, E. spathulata is presently known from western Montana, southern British Columbia and southwestern Alberta. This is a markedly restricted distribution both by comparison to most other species of Encalypta (Horton 1979c) and by comparison to its distribution in Europe. Therefore, I think it probable that the present North American distribution of E. spathulata is relictual and that this species was formerly more widespread on this Continent. Its distribution pattern is similar to a group of species that are tolerant of desiccation, several of which extend as far south as Texas (Schofield 1980). However, E. spathulata appears to be less tolerant of desiccation than some of these species (Horton 1979c). Therefore, it is possible that with the drying of the interior of North America in the Tertiary, southerly populations of E. spathulata became isolated. Encalypta flowersiana may have evolved somewhere in southern Texas or adjacent Mexico in Tertiary times.

Variation: When E. flowersiana was originally described (Horton 1979b), this species was reported to be characterized by a well-defined fringe; however, the more recently discovered population from Texas has the fringe indistinctly defined and more like that described from some populations of E. spathulata. Therefore, it appears that development of the calyptra fringe of E. flowersiana is similarly variable as it is in E. spathulata.

Phylogenetic Relationships: While the structure of the distal surface of spores of E. flowersiana differentiates this species from all other taxa in the E. rhaptocarpa-E.

vulgaris complex, the fundamental similarity in the structure of the two different spore-types is apparent. Therefore, E. flowersiana is considered to belong to the E. rhaptocarpa-E. vulgaris complex. Within this complex, E. flowersiana is most closely related to E. spathulata. As noted under Diagnosis and Differentiation, E. flowersiana is virtually indistinguishable from E. spathulata except in hair-pointed leaves and superficial spore structure.

The striking similarity between E. flowersiana and E. spathulata both structurally and ecologically raises a question as to the taxonomic status of the more recently described taxon. Encalypta flowersiana is presently known from three rather widely separated localities, yet the definitive character-states of spores and leaves are found in populations from all three. There are no collections that appear to be intermediate in the features that differentiate E. flowersiana from E. spathulata. As well, these two taxa are isolated geographically. Therefore, based on structural discontinuity and geographic segregation, the specific status of E. flowersiana is reaffirmed.

Specimens Examined: CANM (2), F (1), FH-Bartram (1), MO (2), MSC (1). annotated key to the taxa. Phytologia 44: 177-214.

ENCALYPTA INTERMEDIA Juratzka in Juratzka et Milde,

Verh. K.K. Zool.-Bot. Ges. Wien 20: 595. 1870.

Figs. 272-276.

Types: "In monte Berytdagh Cataoniae ad 7000' et p. Kharput in rupib. silic. (1865.)" (Lectotype: "Professor C. Haussknecht. Iter orientale 1865 Encalypta intermedia Juratzka sp. nov. Kharput in rup. silic. 4000' dieb. Oct." W!; Syntypes: W-Juratzka (2 specimens, in part)!).

Diagnosis: One of the most characteristic features of E. intermedia is that the seta is so short (1-3 mm long) the calyptra rests on the uppermost leaves. Similarly, the rostrum of the calyptra is short (0.8-1.0 mm long). The opaque calyptra is golden and more-or-less densely papillose with the base of the cylinder entire. Capsules are gymnostomous and furrowed with pale-orange or orange ribs. Around the mouth of the capsule there is a relatively broad, stiffened band and the cylindric shape of the mouth does not change with age. In almost all of the North American populations the leaves are muticous with a rather inconspicuous costa ending well below the apex; however, in a few populations from northern British Columbia and the Yukon Territory the leaves are apiculate with an excurrent costa. The basal cells are more-or-less prominent with yellow to orange transverse walls that angle out from the costa in a "v"-shape. There are more-or-less prominent verrucae on the distal surface of the spores and some have an indistinct triradiate mark on the proximal surface.

Habitat: *Encalypta intermedia s. str.*, as described above, appears to have very narrow tolerances with respect to habitat, at least in North America. It grows in the crevices of calcareous outcrops, generally on the underside of an overhang.

Variation: *Encalypta intermedia* was described on the basis of specimens collected in Persia and the Caucasus by Haussknecht in 1865. It is quite widespread in North America (Fig. 277), although it is more frequent and abundant in warmer, drier and southerly localities. *Encalypta intermedia* occurs as far northward as Scandinavia in Eurasia, but is most prevalent in Mediterranean regions. It has never been recognized as a distinct species except by the original author, and is seldom mentioned, even as a subspecific entity, in the major European floras. In North America, *E. intermedia* has generally been considered to represent part of the variation inherent in *E. vulgaris* (Coker 1918, Flowers 1938, 1973, Lawton 1971). While *E. intermedia s. str.* (see Diagnosis) is distinct from both *E. rhaptocarpa* and *E. vulgaris*, there is a taxon that occurs throughout the range of *E. intermedia* in North America that combines features of both *E. intermedia* and *E. rhaptocarpa*. The seta is always short, as in *E. intermedia*, but a peristome is present in some populations and the leaf apex is either muticous or hair-pointed. Furthermore, this taxon occurs in a different habitat than *E. intermedia s. str.*. Generally, it is not associated with rock outcrops, but occurs on soil in treeless, exposed habitats in prairie or tundra regions. Also, the substrate may be calcareous, but it is frequently subneutral. Many

Figures 272-275. Encalypta intermedia Spores. Scale=5 μm.

Figs. 272-273. North American population.

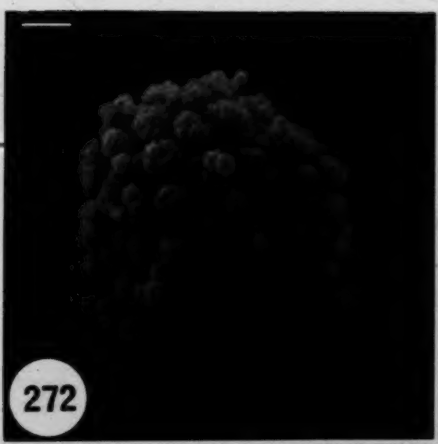
Fig. 272. Distal surface.

Fig. 273. Proximal surface.

Figs. 274-275. Turkish population.

Fig. 274. Distal surface.

Fig. 275. Proximal surface.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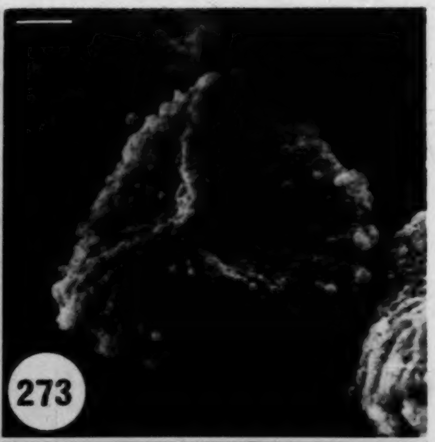
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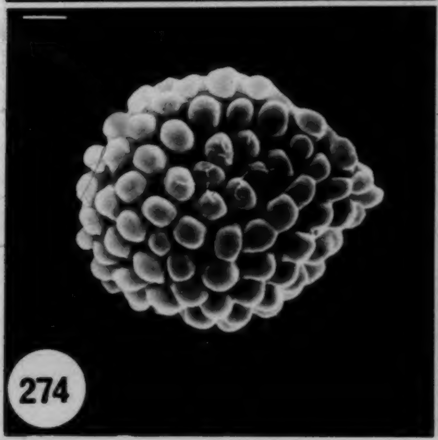
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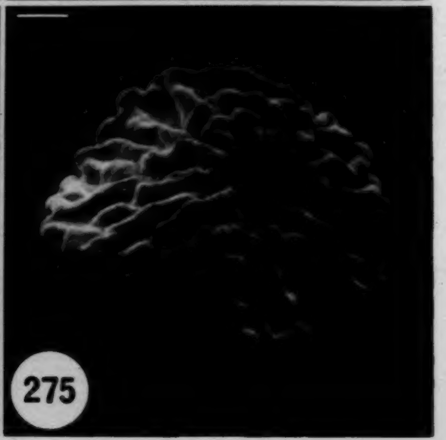
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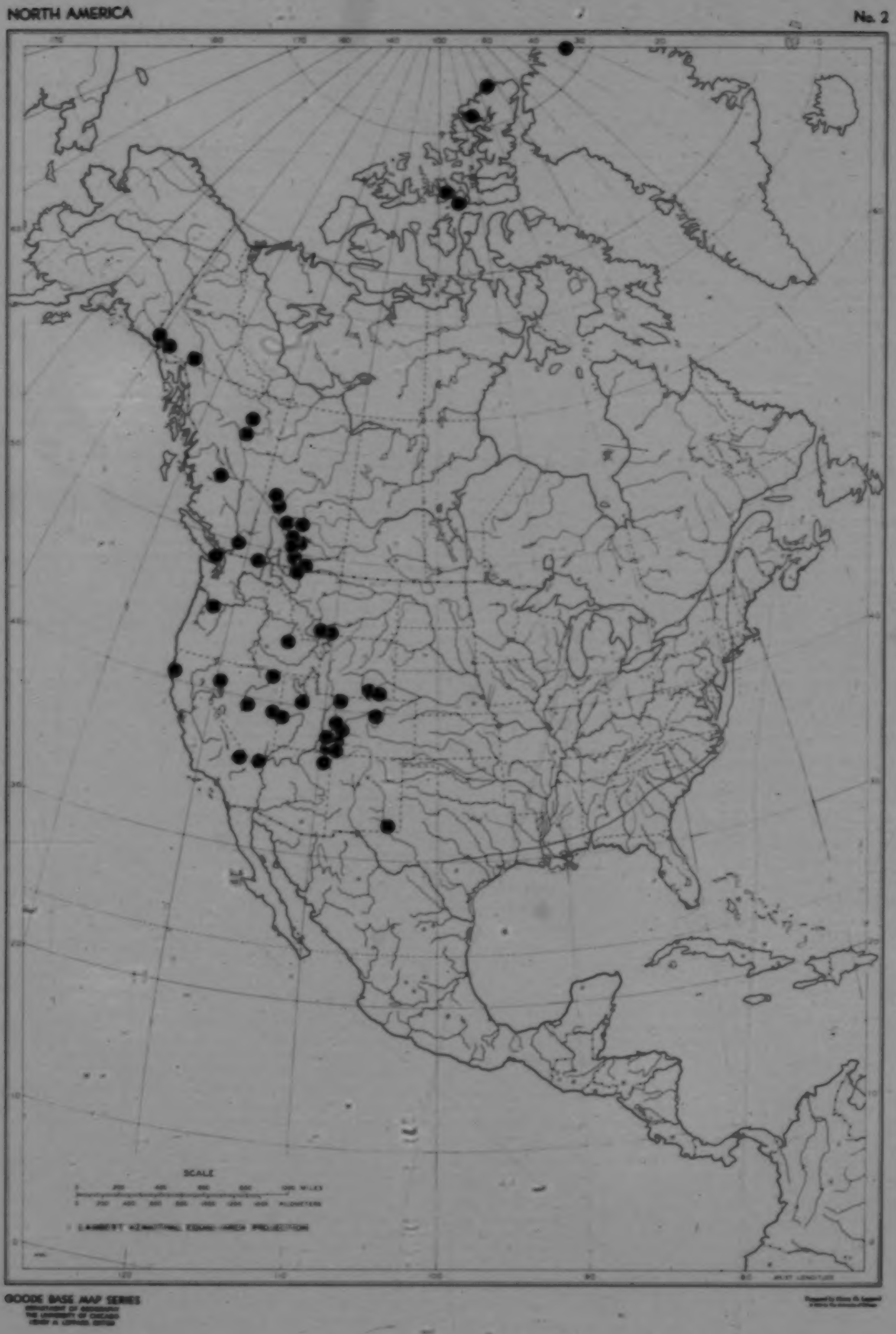
Figure 276. Distribution of *Encalypta intermedia* in North America.


NORTH AMERICA
No. 2
SCALE
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 1200 1400 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
GOODE BASE MAP SERIES
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populations of this taxon are difficult to differentiate from those of E. intermedia and from stunted arctic and antarctic populations of E. rhaptocarpa. Studies are in progress to determine if this taxon is an environmental modification of E. intermedia or if it is a distinct entity.

ENCALYPTA VULGARIS Hedwig,

Spec. Musc. 60. 1801.

Figs. 242, 277–280.

Types: No types cited; reference made to previous publications. (Lectotype: "Bryum extinctorium anthera erecta oblonga minori, calyptris laxis aequalibus. Linn. Sp. pl. 2. p. 1581. 5. Bryum calyptra extinctorii forma minus Dill. Musc. 349. t. 45. f. 8. Enc. vulgaris Hedw. St. Crypt. p. 46. t. 18." G–Hedw.–Schwaegr.!).

Diagnosis: The most striking feature of E. vulgaris s. str. is the shiny, golden–brown costa that forms a prominent keel on the abaxial surface of the leaf almost to the apex. Encalypta vulgaris is also characterized by a more–or–less opaque, pale–golden calyptra with a well–defined, narrow rostrum. The base of the cylinder is either erose or entire. Capsules are smooth to delicately striate and lack a peristome. The seta is moderately long (generally 4–7 mm) and yellow to orange or red. Leaves are muticous with inconspicuous basal cells, which extend outwards from the costa at a "v"–shaped angle. There are more–or–less prominent verrucae on the distal surface of the spores and narrow, radial plicae on the proximal surface.

Variation: See discussion under E. rhaptocarpa.

Figures 277-280. ***Encalypta vulgaris*** **Spores.**

Figs. 277 & 279. Distal surface.

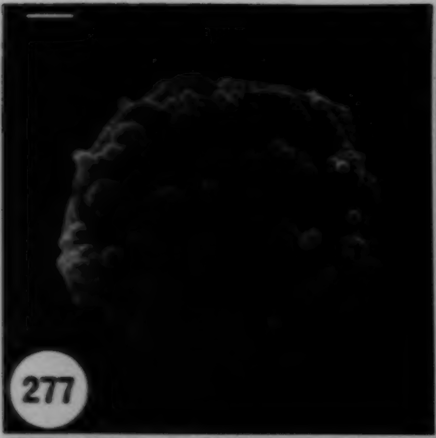
Fig. 277. Scale=5 μm.

Fig. 279. Scale=1 μm.

Figs. 278 & 280. Proximal surface.

Fig. 278. Scale=5 μm.

Fig. 280. Scale=1 μm.



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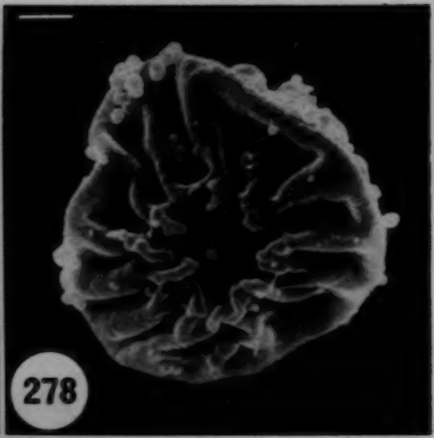

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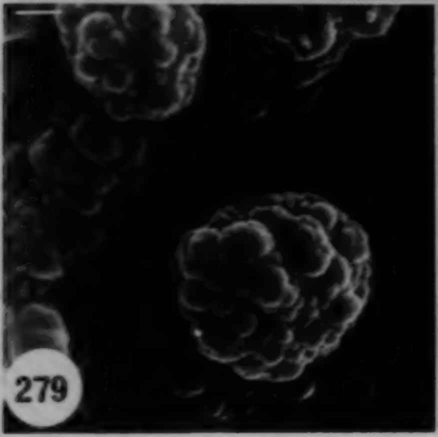

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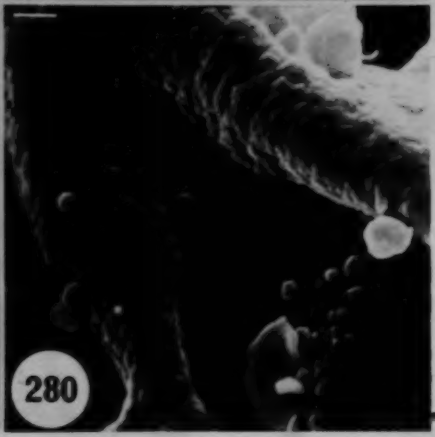

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ENCALYPTA ASPERIFOLIA Mitten,

J. Linn. Soc., Bot. 12: 181. 1869.

Figs. 281–290.

Types: "Andes Quitenses, in saxis prope oppidum Guano (9000 ped.), *Spruce*, n. 150*b*. Andes Peruvianae, Cerro Pasco, *Mathews*." (Lectotype: "E. asperifolia Mitt. M. A. Am 181 Huano Spruce '*Guano*'. no 150b" NY-Mitt.!; Isotypes: BM!, H-Sol!; Possible Isotype: BM-Hook.!; Syntype: NY-Mitt.!).

Encalypta emersa C. Müller, Linnaea 42: 354. 1879. Type "Argentinia subtropica, Cuesta de Pinos inter *Bartramiam strictiusculam* ined., 27. Majo 1873, c. fruct. maturis." (Specimen not found – destroyed in B?).

Encalypta vernicosa Schimp. *ex* C. Müll., Nuovo Giorn. Bot. Ital. 4: 49. 1897. Type: "Bolivia, prov. Larecaja, Sorata, Apacheta de Chuchu, reg. alpina, 4500 m. alta, Martio 1856: *G. Mandon*. Collect. Nº. 1626." (Lectotype: "G. Mandon. Plantae Andium Boliviensium. Nº. 1626 Encalypta vernicola Schpr. Hab. Prov . Larecaja Viciniis Sorata: Apacheta de Chuchu, in scopulosis. Alt. Reg. alpina. 4500 . Mart. 1856." BM-Hook.!; Isotypes: BM-Schimp.!, G-DC.!).

Nomenclatural Notes: (1) The potential isotype of *E. asperifolia* in De Candolle's herbarium ("Spruce. Musci Amazonici et Andini. No. 150(b)") is a *Tortula* species. Therefore, it is not considered part of the type.

(2) Although the specific epithet of *E. vernicosa* is mis-spelled as vernicola on the specimen in Hooker's herbarium and that in De Candolle's herbarium, the rest of the label information corresponds precisely to that published by Müller (1879). In contrast, while the epithet is correctly spelled on the specimen in Schimper's herbarium, the collection number is different and the label information includes only "Encalypta vernicosa Schpr Bolivia Chuchu. Mandon 62. 14 Mars 56". Therefore, I have selected as the lectotype a specimen in Hooker's herbarium because it seems most likely that Müller based his description upon one of these exsiccata specimens. It seems possible that the collection number cited on the specimen in Schimper's herbarium is an error for 1626, as cited in

the original description. Therefore, this specimen is probably an isotype.

There is a second specimen from Chuchu Bolivia in Schimper's herbarium. Presumably this is a duplicate of the isotype of *E. vernicosa* cited above because the locality and data are the same, although the collector's name and number are not cited on this specimen. This collection is designated *E. lampromiticum*, but the name was never published.

(3) I have been unable to trace a specimen of *E. emersa*, but it is considered synonymous with *E. asperifolia* on the basis of the original description. Müller described muticous leaves with a scabrous costa. This combination of features characterizes neither *E. armata*, *E. ciliata* nor *E. rhaptocarpa*, which are the other species of *Encalypta* known to occur in this region of South America.

Diagnosis and Differentiation: There is more interpopulational variation in taxonomically important characters of *E. asperifolia* than in most Encalyptaceae, except in some other taxa in the *E. rhaptocarpa-E. vulgaris* complex. The most reliable combination of features to identify *E. asperifolia* is the puckered, more-or-less scabrous and papillose calyptra with a short fringe of very narrow segments that are also papillose in some populations (a feature that I have not observed in any other species of *Encalypta*), the gymnostomous capsule, muticous leaves with a prominent, golden to dark-brown costa, and spores with large, warty protuberances on the distal surface. Some microscopic features also seem less subject to variability. The basal cells form a fairly extensive, well-defined group with the longitudinal and transverse walls generally dark-orange. A marginal border of five to eight rows of cells is differentiated adjacent to the basal cells and the papillae on the abaxial walls of the transitional cells extend down to the basal cells.

Encalypta asperifolia might be confused with three other species of *Encalypta* that are presently reported from South America, *E. armata*, *E. ciliata* or *E. rhaptocarpa*, or with two others, *E. flowersiana* known from southern North America and Central America, and *E. vulgaris* known from southwestern North America in the New World. *Encalypta armata* parallels those forms of *E. asperifolia* with a calyptra with a short rostrum, a furrowed and ribbed capsule, and a very short seta. It is best differentiated by the long spines (up to 165 μm long) on the back of the costa. By comparison, in *E.*

Figures 281-285. Encalypta asperifolia Spores. Scale=1 mm.

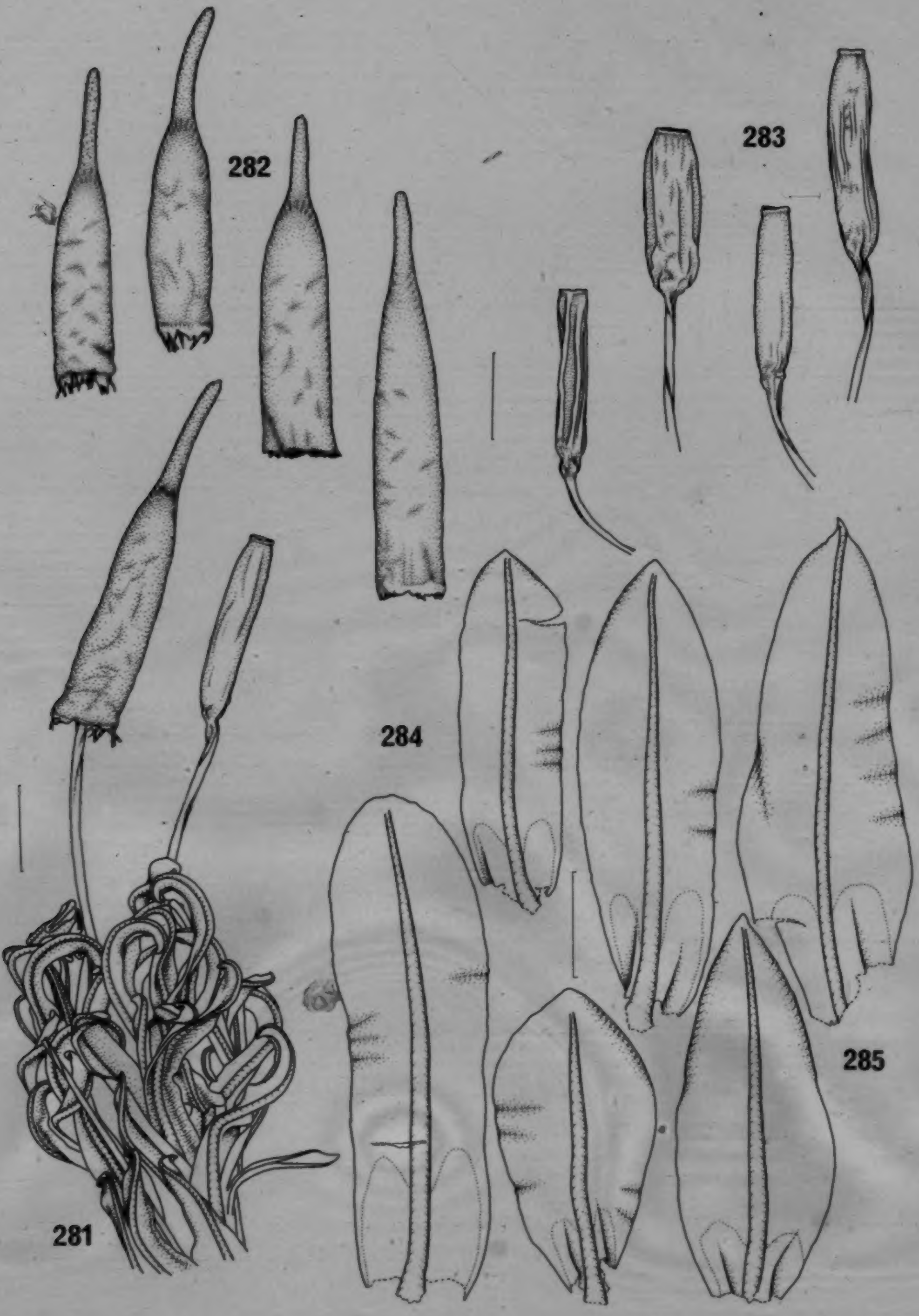
Fig. 281. Habit.

Fig. 282. Calyptrae.

Fig. 283. Capsules.

Fig. 284. Vegetative Leaves.

Fig. 285. Perichaetial leaves.



Figures 286-289. Encalypta asperifolia Spores.

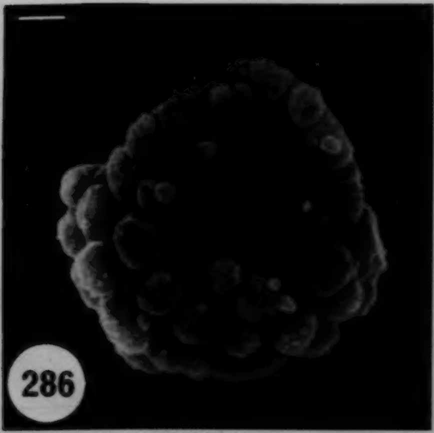
Figs. 286–288. Scale=5 µm.

Fig. 286. Distal surface.

Fig. 287. Proximal surface.

Fig. 288. Tetrad.

Fig. 289. Proximal surface. Scale=1 µm.



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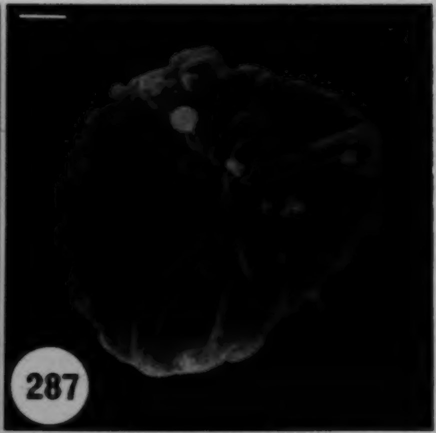

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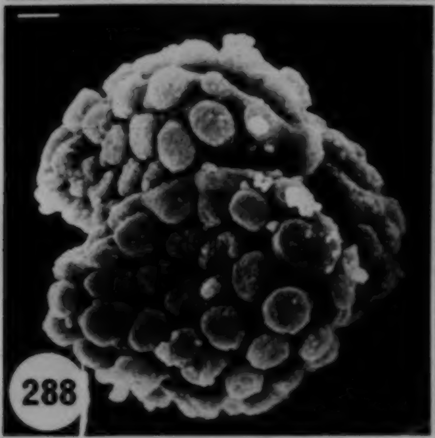

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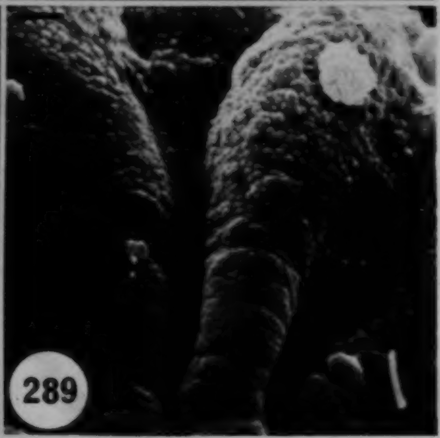

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asperifolia the longest scindulae are only 46(80) μm long. Also, in *E. armata* there are no papillae on the back of the costa, the papillae on the transitional cells do not extend down to the basal cells and the basal cells are less clearly defined because the walls are pale in color by comparison to those of *E. asperfolia*. More subtle differences are that the rostrum of the calyptra in *E. armata* appears narrower and more distinctly defined than that of *E. asperifolia*, and the calyptra, capsule and leaves of *E. armata* tend to be shorter, thus the plants appear smaller than those of *E. asperifolia*.

The fringed calyptra of *E. ciliata*, the smooth capsule and leaves with a prominent, golden or dark-brown costa that is smooth give these plants a facies that strikingly resembles some populations of *E. asperifolia*. Many South American populations of *E. ciliata* have a more-or-less well-developed peristome and the costa excurrent as a mucronate tip; neither of these features occurs in *E. asperifolia* (one population with leaves with a short, blunt mucro was observed, but the mucronate tip was formed by the lamina, not the costa). All populations of *E. ciliata* have the leaf margins recurved in the lower one-half when moistened and when dry. In *E. asperifolia* some leaves are narrowly reflexed in the lower one-half when dry, but they are always plane when moist. Spores of *E. ciliata* lack the warty protuberances characteristic of *E. asperifolia* and are defined by prominent plicae that radiate out from a more-or-less distinct central depression on the distal surface.

In South America some forms of *E. rhaptocarpa* have a peristomate capsule and hair-pointed leaves, so are quite distinct from *E. asperifolia*. However, other forms with a gymnostomous capsule that is furrowed and ribbed, and leaves that are muticous are more difficult to distinguish, particularly since they have the same spore-type as *E. asperifolia*. These are best differentiated by the smooth calyptra that is entire or erose at the base and lacks any suggestion of a fringe, and the costa that hardly keels the leaf and is green to reddish-brown in color.

Encalypta flowersiana is superficially similar to *E. asperifolia* in the fringed calyptra, gymnostomous, furrowed capsule, short seta and muticous leaves, but the spores with vermiform protuberances on the distal surface are quite different.

Encalypta vulgaris is very difficult to differentiate from *E. asperifolia* as the two taxa parallel one another in a number of important characteristics. The scabrous costa that defines many populations of E. asperifolia does not occur in E. vulgaris and the calyptra in E. vulgaris is either entire or erose at the base, not fringed as in E. asperifolia.

Description: Plants to 40 mm tall, yellow- to olive-green above, brown below, ± branched. Stem in transverse section with central strand present but indistinct. Brood bodies absent. Axillary hairs sparse. Leaves when dry incurved and regularly dextrorsely twisted or irregularly contorted, laminae conduplicate, apex ± cucullate; 3.0–5.0 mm long, 1.0–1.5 mm wide, oblong, some ± constricted in the middle, to obovate- or ovate-oblong, apex broadly acute to obtuse, muticous or (in few) broadly mucronate; margins plane to narrowly reflexed in the lower half when dry in some. Costa subpercurrent, ends 7–15 cells below apex, or percurrent, abaxial surface prominently keeled, ± shiny in the upper half, dull basipetally, yellow to dark-brown, smooth to scindulose in the upper half and papillose basipetally, scindulae up to 46(80) µm long, hollow basipetally, papillae tall, some "o"-shaped, much-branched; in transverse section with 3–4 rows of ventral cells, begleiters differentiated in small cluster, lumina small, 8–9 rows of stereids. Upper laminal cells 12–18(20) µm wide, 12–20 µm long, with 5–8 papillae per cell, each ± "c"-shaped; upper marginal cells 14–16 µm wide, 9–12 µm long; transitional cells with walls on abaxial surface papillose to basal cells, papillae larger than on upper cells with longer branches, not "c"-shaped, on adaxial surface walls smooth above basal cells; basal laminal cells 14–50 µm long, 12–20 µm wide, in large, prominent, group, transverse walls dark-orange to orange, longitudinal walls dark-orange to orange, superficial walls smooth except on abaxial surface near transitional cells, entire or irregularly ± perforated; basal marginal cells distinctly differentiated in 5–8 rows. Autoicous. Perichaetial leaves broadly ovate- or elliptic-oblong, apex broadly acute to (in few) broadly mucronate; perigonial leaves 0.9–1.0 mm long, broadly sheath-like below, quickly narrowed to acute apex; perigonial paraphyses with cell walls smooth.

Seta 1–5 mm long, erect to flexuose, slightly twisted dextrorsely just below capsule, shiny, yellow or orange to red near capsule, to dark-red; in transverse section 150 µm in diameter. Capsule (1.8)2.7–3.5 mm, when dry cylindric and smooth or ± longitudinally furrowed, contracted to mouth or ± constricted just below mouth, slightly twisted and puckered, abruptly contracted to seta, pale-golden, some with orange ribs, narrow red rim at mouth, when old ± strongly furrowed; *exothecial cells* 70–140 μm long, 18–23 μm wide, in longitudinal rows, in transverse section superficial walls slightly thickened, more so on capsule ribs; *rim cells* differentiated in 1–3 irregular rows, 7–14(18) μm long, 9–16 μm wide, walls somewhat thickened; *stomata* scattered, 10–13, superficial, 46 μm long, 35 μm wide. *Peristome* absent. *Operculum* plane-convex and rostrate, 1.0–1.3 mm long. *Annulus* undifferentiated. *Spores* brown, heteropolar, 35–44 μm in polar view, 28 μm X 35–44 μm in equatorial view, distal surface with large, hollow gemmae, 2.5–6 μm in diameter, proximal surface with radial plicae, ± granular centrally. *Calyptra* (3.5)4.5–5.2 mm long, extends well below capsule, cylindric to narrowly elliptic-cylindric, ± distinctly contracted to slightly curved rostrum that is (0.9)1.1–1.4 mm long, cylinder puckered throughout, ± constricted basally and fringed, fringe segments short and narrow, readily broken off, calyptra golden to dark-brown distally with rusty streaks or patched on cylinder in many, opaque, somewhat shiny, ± densely papillose including the fringe segments, papillae branched or simple; in transverse section of cylinder 2 rows of cells with small lumina, walls very thick. *Chromosome number* unreported.

Habitat: In my experience, *E. asperifolia* grows in much drier habitats than most other species of *Encalypta*. Otherwise, the habitat is quite typical and populations occur on soil on rock outcrops and in tundra habitats. The data on substrate preferences of *E. asperifolia* are limited, but indicate that it occurs on highly calcareous substrates as well as slightly acidic. Results of analyses of soil samples collected with *E. asperifolia* in the vicinity of Lima are as follows: pH ranges from 6.2 to 7.3 with a mean of 7.0 (n=7); Ca^{++} concentrations range from 156 to 342 ppm with a mean of 236 and s.d. of 74 (n=5); and Mg^{++} concentrations range from 4 to 10 with a mean of 7.2 and s.d. of 2.4 (n=5). The Ca^{++} concentrations are as high as those found for any other species of *Encalypta*, while the Mg^{++} concentrations are strikingly low by comparison to other species of *Encalypta* that occur on substrates with high Ca^{++} concentrations in North America (see Figs. 300–302, Table 9).

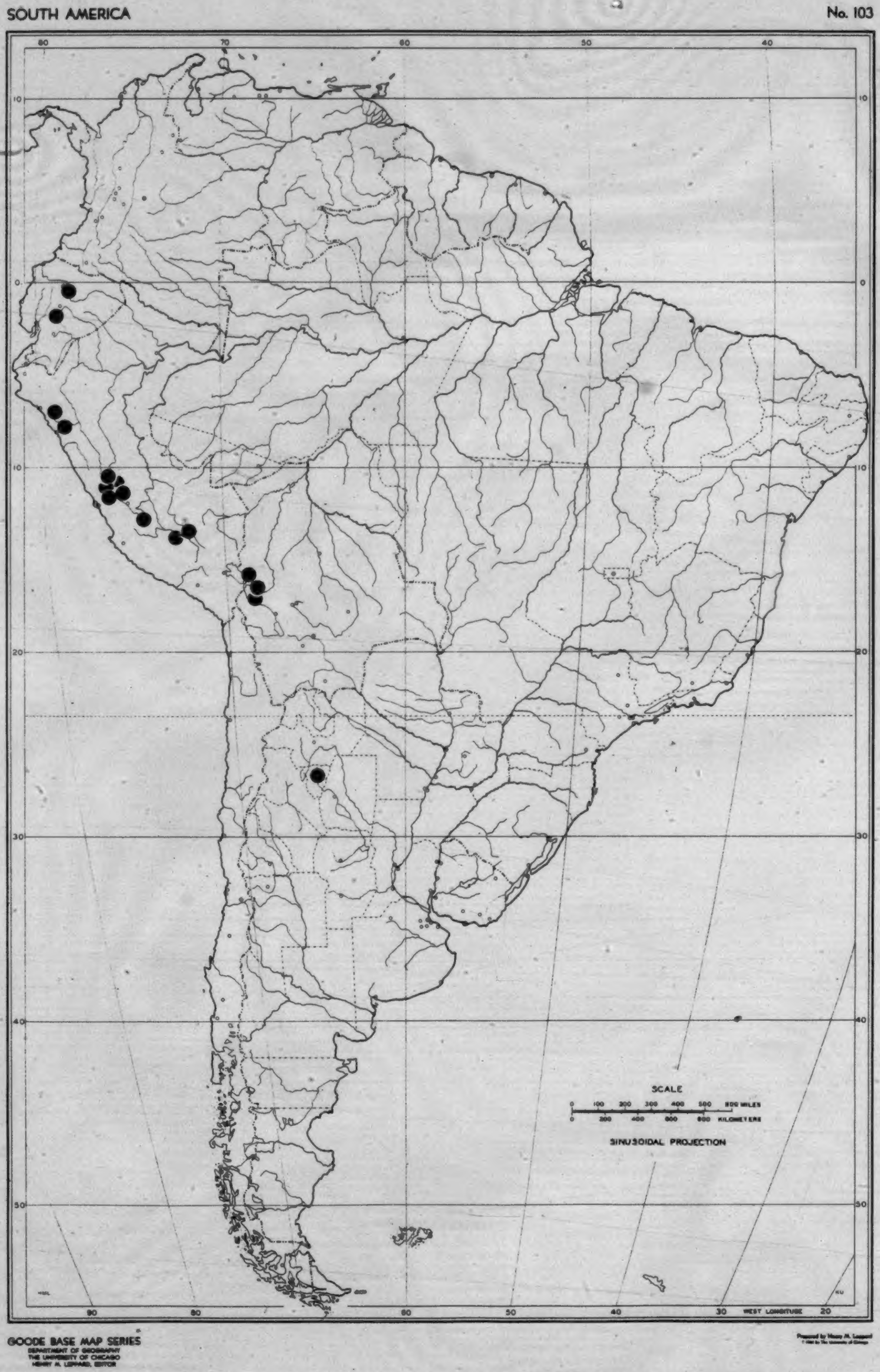
Distribution: *Encalypta asperifolia* is endemic to South America. It is almost certainly restricted to the Andes and is known from Ecuador, Peru, central western Bolivia and Tucuman province of Argentina (Fig. 290).

In the mountains in the vicinity of Lima in Peru, I have found E. asperifolia to be relatively common and the populations are frequently extensive. In all likelihood, it is similarly common throughout its range and the disjunctions between localities (Fig. 290) reflect disjunct collecting localities. Encalypta asperifolia is to be expected from Colombia and Chile, as well as more southerly localities in Argentina.

Variation: As noted above, there is considerable interpopulational variation in E. asperifolia. The rostrum of the calyptra is more-or-less abruptly narrowed from the cylinder, and is moderately long (1.4 mm) in some populations and quite short (1.1 mm) in others. Capsules are either long, smooth and golden or short and more-or-less longitudinally furrowed with orange or red ribs. The seta varies from short (4 mm) to very short (1 mm) and from orange to dark-red. In some populations the costa is perfectly smooth on the abaxial surface, but it is strongly scabrous in others. There are correlations in the occurrence of some of these character-states, but the condition of the costa appears to vary more-or-less independently. Populations with long, smooth capsules have a long-rostrate calyptra and a long seta. Plants with such characteristicis are very difficult to differentiate from E. vulgaris, particularly if the abaxial surface of the costa is smooth and shiny. Specimens characterized by these features have been collected throughout the known range of E. asperifolia. At the other extreme are those populations with short, furrowed capsules, short setae and a short-rostrate calyptra, some of which are very close to E. armata. These are known only from more southerly localities within the range of E. asperifolia. For example, the specimens of E. vernicosa and E. lampromiticum in Schimper's herbarium approach E. armata more closely than most other specimens of E. asperifolia and they are from one of the more southerly localities (Bolivia) for E. asperifolia. The scindulae are up to 80 microns long on the back of the costa, and the calyptrae, capsules and setae are all shorter than in any other populations of E. asperifolia.

The potential taxonomic significance of the existence of forms of E. asperifolia that are structurally similar to E. vulgaris and others that closely parallel E. armata is

Figure 290. Distribution of *Encalypta asperifolia*.


SOUTH AMERICA
No. 103
SCALE
0 100 200 300 400 500 600 MILES
0 200 400 600 800 KILOMETERS
SINUSOIDAL PROJECTION
WEST LONGITUDE
GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR
Prepared by Henry M. Leppard

apparent when the distribution patterns of these three taxa are considered. *Encalypta vulgaris* is presently known from southwestern North America in the New World and *E. armata* is endemic to southwestern South America. In between, *E. asperifolia* ranges through westcentral and northwest South America. Therfore, it might be suggested that *E. asperifolia* represents nothing more than a series of forms that are intermediate between *E. vulgaris* and *E. armata*. However, *E. asperifolia* and *E. vulgaris* are geographically isolated and even the forms of *E. asperifolia* that are most similar to *E. vulgaris* are differentiated by the features noted in Diagnosis and Differentiation. Similarly, the specimens of *E. vernicosa* and of *E. lampromiticum* are characterized by some attributes of *E. asperifolia* that do not characterize *E. armata*. The scindulae are considerably shorter than those found in *E. armata*, the abaxial surface of the costa is papillose below the scindulae, the basal cells are clearly defined by dark-orange walls, and the papillae on the abaxial surface of the transitional cells extend down to the basal cells. Therefore, *E. asperifolia*, *E. vulgaris* and *E. armata* are regarded as specifically distinct.

Phylogenetic Relationships: The warty spores of *E. asperifolia* establish that it belongs to the *E. rhaptocarpa–E. vulgaris* complex. Among the taxa that are characterized by such spores, *E. asperifolia* appears to be most closely related to *E. armata* and *E. vulgaris*. Features that each of these species have in common with *E. asperifolia* are discussed under Diagnosis and Differentiation, and Variation.

Specimens Examined: ALTA (20), B (2), BM (4), F (1), FLAS (3), G (1), H-Sol (1), Priv. Herb. P. & E. Hegewald (17), Priv. Herb. D. G. Horton (7), JE (7), MO (2), NY (5).

ENCALYPTA ARMATA Brotherus in Dusen,

Ark. Bot. 6: 32, pl. 12, figs. 12–14. 1906.

Figs. 291–296.

Type: "Argentina ad coloniam « Los Americanos » haud procul a lacu Nahuelhuapi sitam in fissuris rupium." (Lectotype: "Encalypta armata Broth. Argentina, lac. Nahuelhuapi in fissuris rupium. julio 7a. 1897. P. Dusén." H-Br!; Isotypes: PC!, S-Dusén!).

Encalypta berthoana Ther., Rev. Chilena Hist. Nat. 27: 10, pl. 11, figs. 3a–c. 1923. Type: "Cajon del Cepo, Cordillera de las Condes (leg. Bertho, oct. 1919)." (Lectotype: "122. Encalypta Berthoana Ther. sp. nov. Chile: Cajon del Cepo Cordillera de las Condes (Santiago) leg. P. M. Bertho, oct. 1919" PC!; Isotypes: H-Br!, W!).

Nomenclatural Notes: Dr. Pekka Isoviita has kindly informed me (in litt.) that there is a letter (dated March 9th, 1906) in Helsinki University Library from Per Dusén thanking Brotherus for the description of E. armata. Therefore, Brotherus is considered to be the author of the description and the citation is E. armata Broth. in Dusén, rather than E. armata Broth. ex Dusén.

Diagnosis and Differentiation: The most striking feature of E. armata is that the back of the costa is covered by long, spiny projections (up to 165 μm long). Presumably, these hyaline spines provided the inspiration for the specific epithet, although they are silky and quite harmless in appearance. Shorter spines occur on the rostrum of most calyptrae, but a few are quite smooth. Encalypta armata is also characterized by the pale, transluscent calyptra with a short, well-defined rostrum. The base of the cylinder is slightly constricted and most are erose, but there are one or two in the collections available that have some short segments suggesting that a fringe is present initially. The capsules are longitudinally furrowed with the ribs colored orange in some and while there is no peristome per se a narrow rim of whitish tissue occurs just inside the mouth of the capsule. This tissue is divided longitudinally into truncated segments and is very sparsely papillose on the outer surface so it presumably arises from peristomial layers. In E. armata the seta is very short, approximately one or one and one-half millimetres long.

The short, broad leaves with a rounded, muticous apex have a relatively small group of basal cells that are inconspicuous because the transverse walls are very pale in color. The walls of the transitional cells are smooth well above the basal cells and there is a broad, basal marginal border. The brown, heteropolar spores have large, gemmate protuberances on the distal surface, as are characteristic of the *E. rhaptocarpa–E. vulgaris* complex.

The distinctive "warty" spores of *E. armata* readily differentiate it from most other species of *Encalypta*, except those in the *E. rhaptocarpa–E. vulgaris* complex. Within this group, the long spines on the abaxial surface of the costa separate *E. armata* from all other taxa. The only confusion might be with *E. asperifolia*, some populations of which have very short spines on the back of the costa. However, there are also papillae on the costa in the region of the transitional cells and these do not occur in *E. armata*. Also, in *E. asperifolia* the basal cells are prominently colored and the papillae on the abaxial surface of the transitional cells extend down to the basal cells.

Description: *Plants* to 13 mm tall, green to olive-green above, yellow-brown to brown below, ± branched. *Stem* in transverse section with central strand undifferentiated. *Brood bodies* absent. *Axillary hairs* sparse. *Leaves* when dry appressed, incurved and ± twisted irregularly, laminae incurved to conduplicate; 2.0–3.5 mm long, 1.0–1.4 mm wide, lingulate or ovate-lingulate to oblong, ovate-oblong or lingulate-spathulate, apex rounded, slightly retuse in some, muticous; *margins* plane. *Costa* subpercurrent, ends 3–6 cells below apex, or percurrent, abaxial surface prominently keeled, somewhat shiny, golden to brown, covered particularly in upper two-thirds with long spinose projections, up to 165 μm long, simple and hollow basipetally, few shortly branched apically, ± smooth basipetally; in transverse section with 2–3 rows of ventral cells, begleiters undifferentiated, 3–4 rows of stereids. *Upper laminal cells* 14–18 μm wide, 14–18(25) μm long, with 4–6 papillae per cell, each ± "c"-shaped; *upper marginal cells* 16–18 μm wide, 9–14 μm long; *transitional cells* with walls on both surfaces smooth well above basal cells; *basal laminal cells* 23–58 μm long, 14–20 μm wide, in small, inconspicuous group, transverse walls yellow to pale-yellow, longitudinal walls hyaline, superficial walls smooth, entire or irregularly ± perforated; *basal marginal cells* in broad band. Autoicous.

Figures 291-295. **Encalypta armata.** Scale=1 mm.

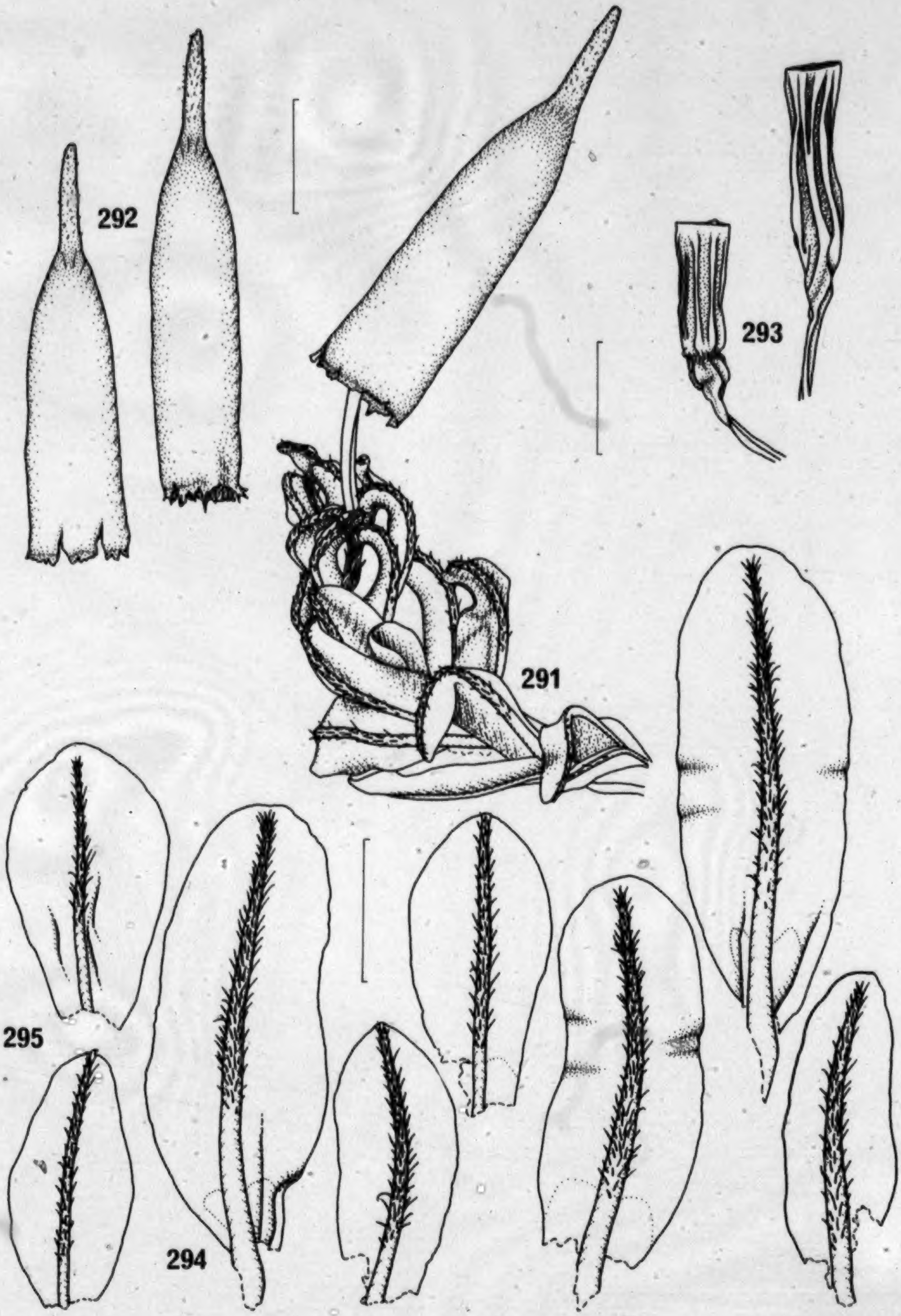
Fig. 291. Habit.

Fig. 292. Calyptrae.

Fig. 293. Capsules.

Fig. 294. Vegetative leaves.

Fig. 295. Perichaetial leaves.



Perichaetial leaves lingulate-spathulate to lingulate-elliptic, apex muticous, very shortly mucronate in few; perigonial leaves 0.9 mm long, broad and sheath-like, quickly narrowed to broadly acute, muticous apex; perigonial paraphyses with walls smooth.

Seta 1.2-1.5 mm long, erect, slightly twisted dextrorsely near capsule, shiny, orange to red, darker near capsule; in transverse section 120 µm in diameter. Capsule (1.2)1.8-2.2 mm long, when dry cylindric and longitudinally furrowed, ± constricted in lower part then puckered and quickly narrowed to seta, pale-golden to golden, some with orange ribs, narrow red rim at mouth; exothecial cells 46-92 µm long, 16-35 µm wide, in longitudinal rows, in transverse section superficial walls thin or somewhat thickened on ridges, 9 µm thick; rim cells differentiated in 1-2 irregular rows, 7-12 µm long, 12-16 µm wide, walls somewhat thickened; stomata scattered, 7, superficial, 30-39 µm long, 35-44 µm wide. Peristome absent or vestigial and consists of very narrow rim of white tissue divided into truncated segments. Operculum not observed. Annulus undifferentiated. Spores brown, heteropolar, 32-37 µm in polar view, 25 µm X 32-37 µm in equatorial view, distal face with large, gemmate protuberances, 3-7 µm in diameter, proximal face with fine radial plicae and centrally an extraneous granular deposition. Calyptra 3,0-4.5 mm long, extends well below the capsule, distinctly contracted to slightly curved rostrum that is 0.9-1.0 mm long, constricted or contracted at base of cylinder, ± erose, narrowly lacerate or fringed, fringe segments short and narrow, calyptra pale-golden to dark-brown at tip of rostrum, transluscent, shiny, smooth throughout or with short spiny projections on rostrum and smooth basipetally; in transverse section of cylinder with 2 rows of cells with small lumina, walls very thick. Chromosome number unreported.

Habitat: The only habitat information presently available for E. armata is the notation on the type collection "...in fissuris rupium."

Distribution: Encalypta armata is endemic to South America and is presently known from only two localities on the basis of the type collections of E. armata and E. berthoana. The former is from Lake Nahuel Huapí in western Argentina very near the Chilean border and the latter is from Las Condes along the Molina (or Cepo) River close to Santiago, Chile

(Fig. 296).

Phylogenetic Relationships: The warty spores with hollow gemmae indicate that E. armata belongs to the E. rhaptocarpa-E. vulgaris complex. Within this group, the calyptra with a well-defined rostrum and erose base with short segments suggestive of a fringe are features shared with E. asperifolia. As well, some populations of E. asperifolia are characterized by short spines on the back of the costa, a features known to occur in no other species of Encalypta. The prominent, brown or yellow costa of E. armata and the muticous leaves are both features that might indicate a relationship with E. vulgaris, while the furrowed and, in some instances, ribbed capsules occur in E. rhaptocarpa, E. intermedia, E. spathulata and E. flowersiana.

Specimens Examined: H-Br (2), PC (2), W (1).

Figure 296. Distribution of *Encalypta armata*.

SOUTH AMERICA **No. 103**

GOODE BASE MAP SERIES
DEPARTMENT OF GEOGRAPHY
THE UNIVERSITY OF CHICAGO
HENRY M. LEPPARD, EDITOR

Prepared by Henry M. Leppard
[illegible]

IV. PHYLOGENETIC TREATMENT

A systematic treatment should not be regarded as complete without a consideration of the kinship relations among the taxa within the group of organisms being studied. Furthermore, relationships with other groups of similar organisms should also be evaluated. A systematist learns a great deal more about the taxa that he is working with than just how to differentiate them. A great part of what he has learnt is an understanding of the taxa relative to one another and to other closely related groups. The value of such knowledge as a stimulating basis for future research can not be underestimated and such data should not go unrecorded.

It is often stated that inferences about evolutionary relationships cannot properly be drawn without data from the fossil record on which to base them. As with most extant Bryidae, the Encalyptaceae are known no earlier than Pleistocene times from subfossil deposits (see Introduction – Historical Perspective). However fossils must be interpreted in much the same way that extant plants are. The fossil record only indicates a small portion of what existed at a particular point in time. The occurrence of one structure in the fossil record and the absence of another, in itself says nothing about which is the derived state. The fossil record rarely gives us data about plesiomorphous and apomorphous states at a particular point in time. Therefore, the paleobotanist and the taxonomist alike must study different structures to try and determine what the plesiomorphous and apomorphous character-states are in order to reconstruct the evolutionary pathways. The most likely sources of misinterpretation in the pursuit of this objective are instances of convergent evolution, that is, the independent acquisition of the same character-state in two taxa, and character-state reversals, that is, a character-state that is generally plesiomorphous, but that is also secondarily apomorphous, in some instances. In order to avoid such pitfalls, the systematist must search for a character or characters that are so complex in their structure that he can be reasonably sure that they are not likely to have evolved in exactly the same form more than one time. Such characters are generally less influenced by selection pressures and therefore more stable through time. With such a character for a basis, the systematist can then search for correlations in other characters to determine the directions of evolution. In this way, character-states that have undergone convergent evolution or reversal can hopefully be detected and avoided. The systematist can then by inference suggest the evolutionary relationships among the taxa and with other groups, and the implications of these can be assessed.

The peristome that occurs in the Musci is a complex, seemingly stable structure. Even in the earliest bryological literature, the peristome is a prominent character in keys and groupings of species. However, Philibert (1884) firmly entrenched the idea that peristome structure must be the ultimate basis for determining natural affinities among mosses.

> "Les caractères du péristome me paraissent avoir une importance supérieure à celle de tous les autres pour la détermination des affinitiés naturelles dans les mousses; je crois que c'est seulement par la comparaison de ces caractères que l'on pourra arriver à former quelques conjectures vraisemblables sur l'origine et l'évolution des différents types de cette classe. La structure du péristome, en effet, présente une constance frappante et souvent une similitude complete dans une multitude d'espèces très-différentes d'ailleurs par tous les caractères du système végétatif, et que l'on souvent placées dans des tribus très-éloignées. Il est cependent extremement probable que toutes ces espèces, qui ont un péristome presque identique, ont une origine commune, soit qu'elles soient issues les unes des autres, soit qu'elles derivent de formes actuellement éteintes. Il serait impossible, en effet, de comprendre comment cette structure si complexe quelquefois du péristome et cependant si uniforme se serait produite séparément dans des espèces qui appartiendraient à des séries de formation indépendantes les unes des autres."

The influence of Philibert's ideas has been lasting. One of the primary bases for the major groupings in our present-day classification of mosses is peristome structure (Fleischer 1904, Brotherus 1923-1924, Robinson 1971). Philibert (1884) was the first to state that it is highly unlikely that such an involved structure as the peristome could have evolved independently in the same form. The corollary to this is that the evolutionary trend in peristome development must be one of reduction and, ultimately, the loss of the peristome. Philibert (1884) recognized, as Mitten (1859) had earlier, that those species that lack a peristome are derived from peristomate species. "Les especes a peristome nul ou imparfait ne peuvent pas etre classees a part; elles doivent etre rattachees aux especes a peristome bien developpe dont elles sont le plus voisines par l'ensemble de leur organisation." However, Philibert (1884-1890) did not make it absolutely clear, although it is perhaps implied, that he considered the diplolepideous or, in very simplistic terms, double peristome to be primitive and the haplolepideous or single peristome to be derived. Historically, the Haplolepideae have always been placed initially in classifications. The implication is that the single peristome represents the plesiomorphous condition. Recently, Crosby (1980), in a marked break with bryological tradition, suggested that the Diplolepideae should come first as the haplolepideous peristome is probably the derived condition and Vitt (1981) incorporated this in his new classification of the Musci. Certainly, such an idea is the logical conclusion of Philibert's point that the same peristome-type cannot have arisen more than once.

I consider the structure of the peristome to be of fundamental importance in understanding evolutionary relationships within the Encalyptaceae, and concur that the most plausible interpretation, on the basis of the data presently available, is that reduction in peristome structure is indicative of derivation. A well-developed, double peristome (Fig. 47) is considered to represent the plesiomorphous condition in the Encalyptaceae and the lack of a peristome (Fig. 52) is regarded as highly derived. There are two types of single peristomes that occur in the Encalyptaceae. Those that are composed of several cell layers radially (Figs. 47-49) are considered less derived than those that consist of a single layer (Figs. 50-51). The species with each of the four peristome-types are listed in Table 5. This interpretation of the direction of peristome evolution can be validated by an analysis of the groupings based on characters other than the peristome. On the basis of other, unrelated structural features, those species with a double peristome are most closely related to one another, while those species that lack a peristome are generally more closely related to a peristomate species than they are to one another. Therefore, the gymnostomous condition appears to have evolved independently in several lines within the Encalyptaceae. Realizing that characters do not necessarily evolve synchronously, if the double peristome is considered to represent the plesiomorphous condition, it follows that those taxa with a double peristome may also have retained other plesiomorphous character-states, while those with a derived peristome structure are probably derived in some other respects as well. Therefore, correlations with peristome structure must be sought in other characters.

Many species of Musci have apolar, green, more-or-less papillose spores that are relatively uniform in size (McClymont 1954). There are some exceptions of genera or

Table 5. PERISTOME TYPES IN THE ENCALYPTACEAE
(Symbols in brackets are referred to in tables 5-7).

Plesio.	**Double Peristome:**	*B. longipes*	
	(II)	*E. procera*	
		E. streptocarpa	
	Single Peristome:	*E. affinis*	
	(several layers)	*E. brevicolla*	
	(Ia)	*E. longicolla*	
	Single Peristome:	*E. ciliata*	
	(single layer)	*E. rhaptocarpa*	
	(Ib)	*E. vittiana*	
Apo.	**No Peristome:**	*E. alpina*	*E. intermedia*
	(0)	*E. armata*	*E. microstoma*
		E. asperifolia	*E. mutica*
		E. brevipes	*E. sibirica*
		E. flowersiana	*E. spathulata*
			E. vulgaris

families in which the spore structure is more elaborate, and these mostly occur in groups considered derived on other grounds, for example, the Bruchiaceae. Therefore, it seems safe to assume that isopolar, green spores that are small and have a more-or-less nondescript sculpture represent the primitive condition. As with peristome structure, there is an amazing diversity of spore-types in the Encalyptaceae and the different types correlate quite closely with differences in peristome-type. Those species with a double peristome all have small, green spores that are finely papillose (Fig. 65). Species with a single peristome in several layers all have larger spores that exhibit weak polarity, at least in shape. The ornamentation is variable. Some are finely papillose, but the papillae are ornamented with an elaborate microsculpture, others have larger, gemmate protuberances and some have larger verrucae (Figs. 115-120, 140-148, 161-172). Those species with a single-layered peristome, or that lack a peristome generally have large spores that are distinctly differentiated in both shape and superficial structure, although there are a few with paraisopolar spores. The superficial ornamentation of spores that are heteropolar is quite different on the two surfaces. The species, arranged on the basis of spore type, are listed in Table 6. The peristome-type is indicated in brackets after each species (refer to Table 5). The correlations between peristome-type and spore-type are not absolute (for example, E. alpina, E. brevipes and E. mutica, all of which are species characterized by the lack of a peristome, correlate, on the basis of spore structure, with the group of species characterized by a single peristome composed of several layers); however,, the general groupings are quite close to those based on peristome-type. Those species with a double peristome appear to have spores that represent the plesiomorphous condition.

The basic shape of the calyptra in the Encalyptaceae, that is, a long cylinder terminated by a rostrum, is uniform throughout the family and is one of the few features that unquestionably links Bryobrittonia with the genus Encalypta. Yet, there are a considerable number of variations on this basic form and an analysis of these reveals that calyptra shape is actually the sum of a complex combination of at least four or five different characters. These include length of the calyptra, definition of the rostrum, structure of the base of the cylinder and length of the rostrum, among others. Color of the calyptra is another character in which evolutionary trends are apparent. A comparison

Table 6. SPECIES OF ENCALYPTACEAE ARRANGED ACCORDING TO SPORE TYPE.

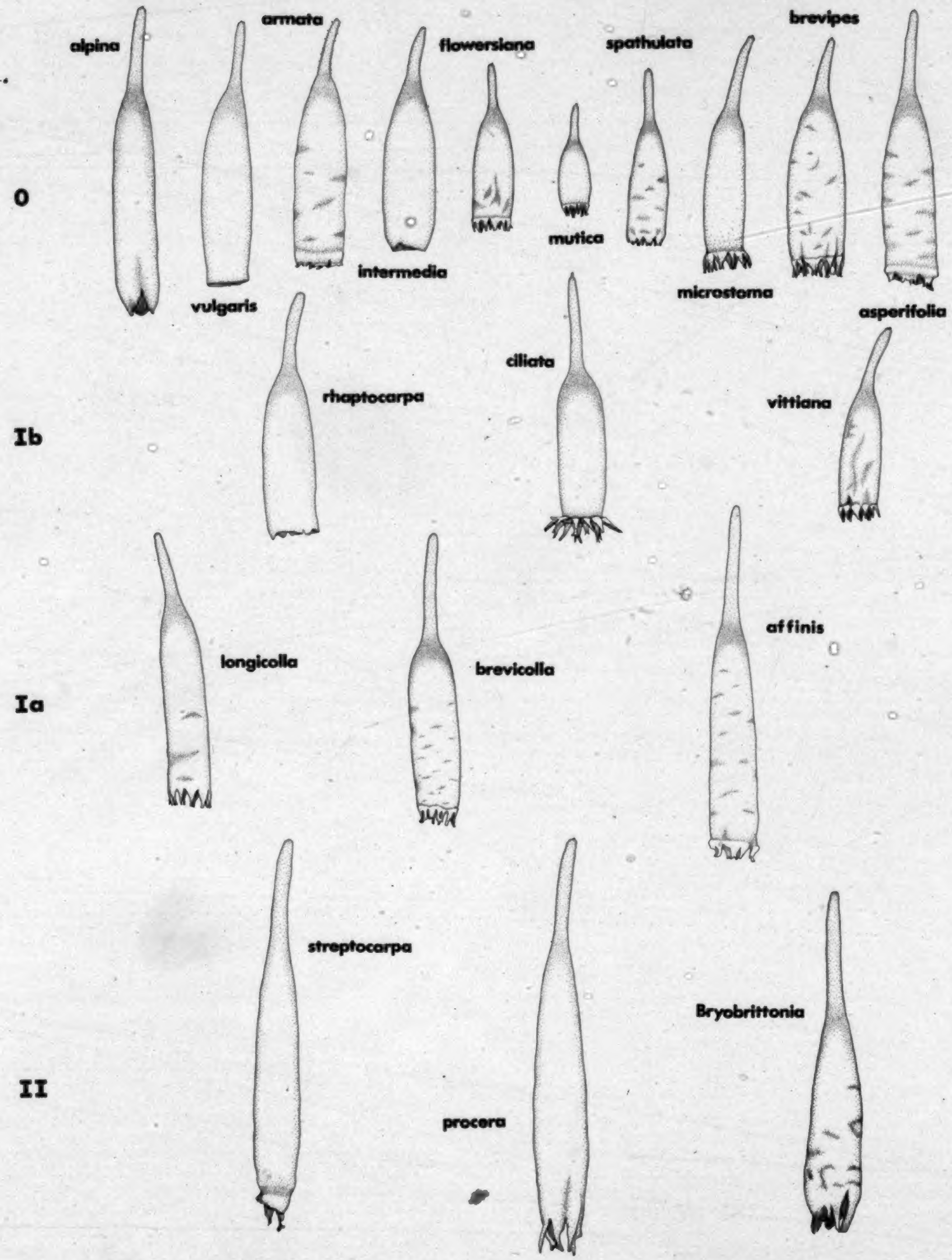
Plesio.	**Isopolar, Small:**	*B. longipes* (II)	
		E. procera (II)	
		E. streptocarpa (II)	
	Paraisopolar, Large:	*E. affinia* (Ia)	
		E. brevicolla (Ia)	
		E. longicolla (Ia)	
		E. alpina (0)	
		E. brevipes (0)	
		E. mutica (0)	
Apo.	**Heteropolar, Large:**	*E. ciliata* (Ib)	*E. intermedia* (0)
		E. rhaptocarpa (Ib)	*E. microstoma* (0)
		E. vittania (Ib)	*E. sibirica* (0)
		E. armata (0)	*E. spathulata* (0)
		E. asperifolia (0)	*E. vulgaris* (0)
		E. flowersiana (0)	

of the different states of each of these characters with the different peristome-types (indicated in brackets) gives an indication of evolutionary trends in each of the calyptra characters (Table 7). A calyptra with all of the plesiomorphous character-states combined would be one that is long, and tapered gradually to a moderately long rostrum. Therefore, the rostrum would be indistinctly differentiated from the cylinder. The base of the cylinder, if the calyptra has not been exposed to the vicissitudes of the environment for too long (in that instance, it becomes eroded away), would be more-or-less longitudinally lacerate into broad segments. The calyptra would be dark, golden-brown in color and so opaque that the capsule would not be visible, or just barely so, through it. Such a calyptra-type is exemplified by that of E. streptocarpa (Fig. 297). From such a primitive type, the evolutionary trends appear to have been towards a shorter calyptra (the calyptrae in Fig. 297 are all drawn to scale) with a well-defined rostrum. That is, the cylinder is quite abruptly contracted to the rostrum (for example, compare the differentiation of the rostrum in E. streptocarpa with that in E. brevicolla, Fig. 297). There appear to have been two different evolutionary trends in length of the rostrum. Apomorphous conditions are considered to be either a very long rostrum (for example, that of E. ciliata, Fig. 297) or a very short one (for example, that of E. brevipes, Fig. 297). It is apparent from the analysis of each of the five characters that character-state evolution has been independent in the different characters. For example, E. alpina has a distinctly defined rostrum that is considered to be an apomorphous character-state; however, the calyptra is relatively long and dark, and the base of the cylinder is lacerate, although the segments are narrower than in E. streptocarpa. All of the latter character-states are considered to represent the plesiomorphous condition. Therefore, E. alpina has retained more plesiomorphous character-states than most other other gymnostomous species of Encalyptaceae (Fig. 297). Also, it appears that some character-state reversals have occurred in the calyptra. For example, the rostrum of E. microstoma is less distinctly differentiated than that of E. ciliata (Fig. 297), yet on the basis of other characters, E. microstoma is almost certainly a gymnostomous derivative of the peristomate E. ciliata. However, the evolutionary trends of a decrease in overall length of the calyptra, an increase in definition of the rostrum, either a decrease or increase in the length of the rostrum, and either the development of a fringe or a rather

Table 7. CHARACTERS OF THE CALYPTRA AND THEIR STATES IN SPECIES OF ENCALYPTACEAE.

	I. Definition of Rostrum	II. Structure of Base of Cylinder	III. Calyptra Length	IV. Rostrum Length	V. Color
Plesio.	Undifferentiated: B. longipes (II) E. procera (II) E. streptocarpa (II)	Lacerate: B. longipes (II) E. procera (II) E. streptocarpa (II) E. longicolla (Ia) E. alpina (0)	Long: B. longipes (II) E. streptocarpa (II) E. procera (II) E. affinis (Ia) E. alpina (0) E. brevicolla (Ia) E. longicolla (Ia)	Moderately Long: B. longipes (II) E. procera (II) E. streptocarpa (II) E. longicolla (Ia) E. rhaptocarpa (Ib) E. vittiana (Ib) E. alpina (0) E. microstoma (0) E. vulgaris (0)	Dark and Opaque: B. longipes (II) E. procera (II) E. streptocarpa (II) E. longicolla (Ia) E. alpina (0)
	Ill-defined: E. affinis (Ia) E. brevicolla (Ia) Distinct: E. rhaptocarpa (Ib) E. vittiana (Ib) E. alpina (0) E. armata (0) E. asperifolia (0) E. brevipes (0) E. intermedia (0) E. microstoma (0) E. vulgaris (0)	Fringed or erose: E. affinis (Ia) E. brevicolla (Ia) E. rhaptocarpa (Ib) E. armata (0) E. asperifolia (0) E. brevipes (0) E. flowersiana (0) E. intermedia (0) E. spathulata (0) E. vulgaris (0)	Short: E. ciliata (Ib) E. rhaptocarpa (Ib) E. vittiana (Ib) E. armata (0) E. asperifolia (0) E. brevipes (0) E. flowersiana (0) E. intermedia (0) E. mutica (0) E. microstoma (0) E. spathulata (0) E. vulgaris (0)	Very Long: E. affinis (Ia) Ebrevicolla (Ia) E. ciliata (Ib) E. sibirica (0)	Lighter and somewhat transluscent: E. affinis (Ia) E. brevicolla (Ia) E. rhaptocarpa (Ib) E. vittiana (Ib) E. armata (0) E. asperifolia (0) E. brevipes (0) E. intermedia (0) E. vulgaris (0)
Apo.	Distinct and narrow: E. ciliata (Ib) E. flowersiana (0) E. mutica (0) E. sibirica (0) E. spathulata (0)	Precisely fringed: E. ciliata (Ib) E. vittiana (Ib) E. microstoma (0) E. mutica (0) E. sibirica (0)		Short: E. armata (0) E. asperfiloia (0) E. brevipes (0) E. flowersiana (0) E. intermedia (0) E. mutica (0) E. spathulata (0)	Pale and transluscent: E. ciliata (Ib) E. flowersiana (0) E. microstoma (0) E. mutica (0) E. sibirica (0) E. spathulata (0)

Figure 297. Correlation Between Calyptra Type and Peristome Type in the Encalyptaceae.


O
alpina
vulgaris
armata
intermedia
flowersiana
mutica
spathulata
microstoma
brevipes
asperifolia
Ib
rhaptocarpa
ciliata
vittiana
Ia
longicolla
brevicolla
affinis
II
streptocarpa
procera
Bryobrittonia

even termination to the base of the cylinder generally correlate with peristome-type (Fig. 297).

There is considerable variation in seta and leaf length in the Encalyptaceae; however, this variation is not random. An arrangement of the species on the basis of different states of these two characters also correlates with the occurrence of different peristome-types (Table 8). Generally, those species with a double peristome also have a long seta and long leaves. Conversely, the character-states of a short seta and short leaves are concentrated among those species that lack a peristome. Therefore, it appears that in the Encalyptaceae a long seta and long leaves, or generally larger plants, represent the plesiomorphous condition. In a general way, this applies to the Musci as a whole, particularly with respect to seta length. For example, species of Bryum appear relatively unspecialized in many other characters and most also have a relatively long seta. In contrast, the ephemeral Pottiaceae and Ephemeraceae that are characterized by a very highly derived life-style have a very short seta.

There are several character-states other than those discussed above that are unique to one or more of the species of Encalyptaceae with a double peristome. These include the occurrence of a well-developed, revoluble annulus in B. longipes, E. procera and E. streptocarpa, the dioicous sexual condition of B. longipes and E. streptocarpa, the consistent occurrence of a central strand in the stem of B. longipes and its sporadic occurrence in E. procera and E. streptocarpa, and the occurrence of begleiter cells in a transverse section of the costa of B. longipes. A well-developed, revoluble annulus is of sporadic occurrence in the Musci, but it is generally found in more primitive groups, for example the Bryaceae, or in more primitive members of particular genera. Lowry (1948) demonstrated a definite correlation between low chromosome number and the dioicous sexual condition in the Mniaceae. It is apparent from Hebant's (1977) work that there is a general trend towards despecialization of anatomical structure in both the stem and costa of mosses. The lack of a central strand and begleiter cells are considered derived conditions. Therefore, the restriction of these plesiomorphous character-states to the three species already shown to have the plesiomorphous condition of peristome, spores and calyptra, as well as seta and leaf length, suggests that B. longipes, E. streptocarpa and E. procera most closely approach the ancestral type in the Encalyptaceae. In the following

Table 8. DIFFERENCES IN SETA AND LEAF LENGTH IN SPECIES OF ENCALYPTACEAE.

	I. Seta Length		II. Leaf Length	
Plesio.	Very Long: (20–38 mm)	*B. longipes* (II) *E. procera* (II) *E. streptocarpa* (II)	Very Long: (6.5–8.0 mm)	*B. longipes* (II) *E. streptocarpa* (II)
	Long: (15–20 mm)	*E. affinis* (Ia) *E. brevicolla* (Ia)	Long: (5.5–6.8 mm)	*E. procera* (II) *E. affinis* (Ia) *E. brevicolla* (Ia) *E. ciliata* (Ib)
	Medium: (10–14 mm)	*E. longicolla* (Ia) *E. ciliata* (Ib) *E. rhaptocarpa* (Ib) *E. alpina* (0) *E. sibirica* (0)	Medium: (3.5–4.5 mm)	*E. rhaptocarpa* (Ib) *E. alpina* (0) *E. asperifolia* (0) *E. brevipes* (0) *E. intermedia* (0) *E. microstoma* (0) *E. sibirica* (0) *E. spathulata* (0) *E. vulgaris* (0)
Apo.	Short: (3–8 mm)	*E. vittiana* (Ib) *E. armata* (0) *E. asperifolia* (0) *E. brevipes* (0) *E. flowersiana* (0) *E. intermedia* (0) *E. microstoma* (0) *E. mutica* (0) *E. spathulata* (0) *E. vulgaris* (0)	Short: (2.0–3.0 mm)	*E. longicolla* (Ia) *E. vittiana* (Ib) *E. armata* (0) *E. flowersiana* (0) *E. mutica* (0)

sections the infrageneric relationships of Encalypta are discussed, and illustrated in a Wagner Dendrogram (Fig. 298) and a Hennig Cladogram (Fig. 299). Intergeneric relationships are discussed, and illustrated in the Hennig Cladogram. The concepts and methodology for phylogenetic analyses according to Wagner are in Wagner (1952, 1962, 1980), while those of Hennig are in Hennig (1950,1965, 1966) and Kavanaugh (1978). The relationships among the taxa are based upon the initial assumption that E. streptocarpa and E. procera most closely approximate the ancestoral type in Encalypta. Lineages are derived from an analysis of the characters discussed above, as well as additional characters.

Inter-relationships Among Species of Encalypta

(1) The E. streptocarpa-E. procera Group. The taxa that comprise the basal group of species in Encalypta, E. streptocarpa and E. procera, are linked by a number of plesiomorphous character-states that occur in no other species, as discussed above. The shape and color of the calyptra, the presence of a well-developed, revoluble annulus, the double peristome, the long seta and the long leaves are some of the features that define the E. streptocarpa-E. procera group. Furthermore, there are additional character-states that suggest a close relationship. For example, in both species the capsule is deeply furrowed, either spirally or longitudinally; however, the color of the ridges is undifferentiated from that of the furrows. The rim at the mouth of the capsule is poorly defined and consists of only one or two, irregular rows of small cells. The stomata are restricted to the base of the capsule where it puckers and narrows to the seta. The relationship between E. streptocarpa and E. procera appears to be very close. This is particularly evident in sterile plants of the two species, many populations of which are virtually inseparable. Also, the masses of filiform brood bodies that occur in the axils of the leaves of sterile plants are found in no other species of Encalypta. An analysis reveals that there are more plesiomorphous character-states in E. streptocarpa by comparison to E. procera, and E. streptocarpa is considered to represent the primitive type within the Encalyptaceae. In several characters, the trend away from the plesiomorphous condition is evident in E. procera. The rostrum of the calyptra is almost undifferentiated from the

Figure 298. Wagner Dendrogram Illustrating the Inter-relationships Among the Species of Encalypta as Determined by an Analysis of Trends in Character-state Evolution.

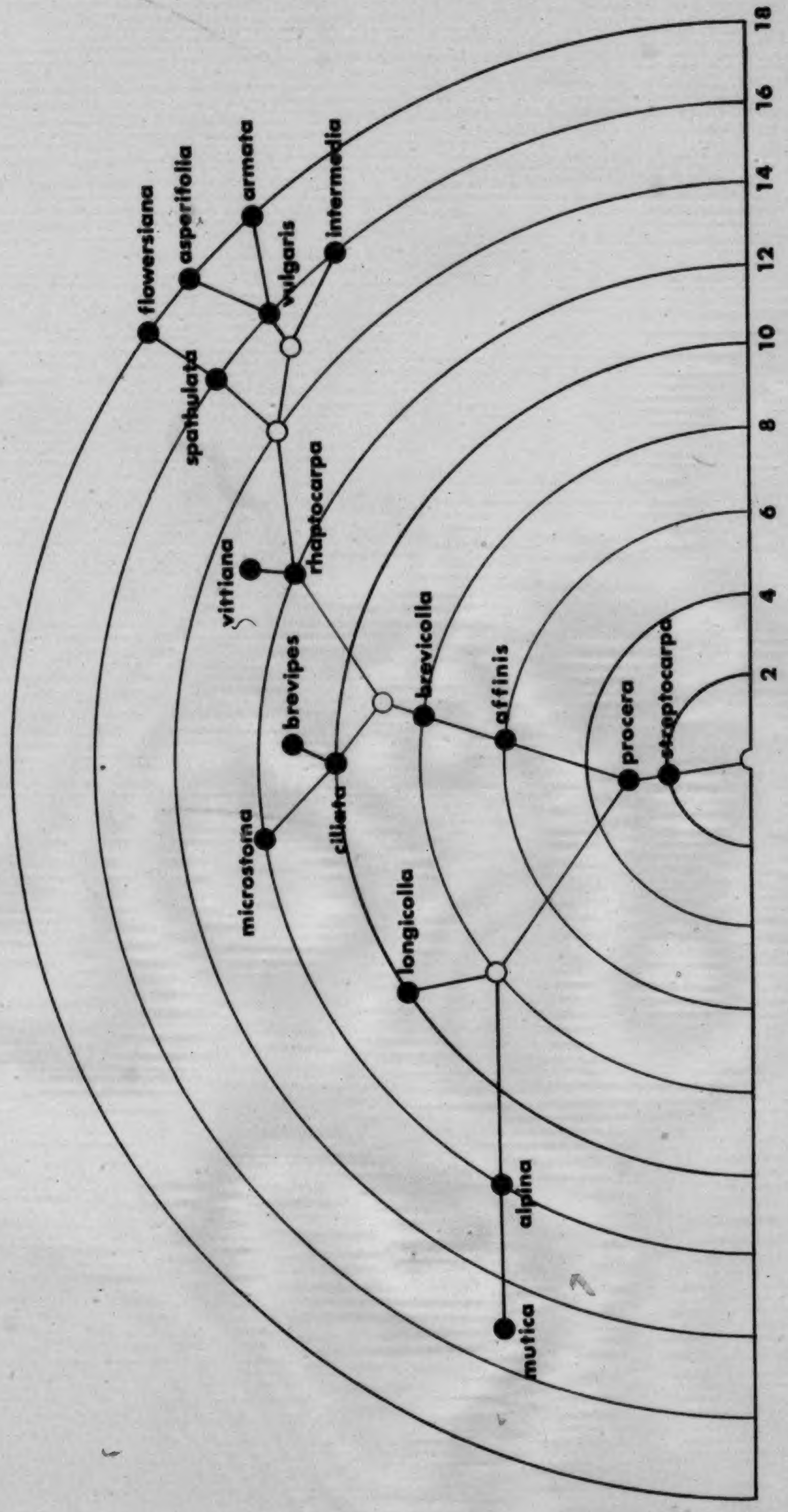
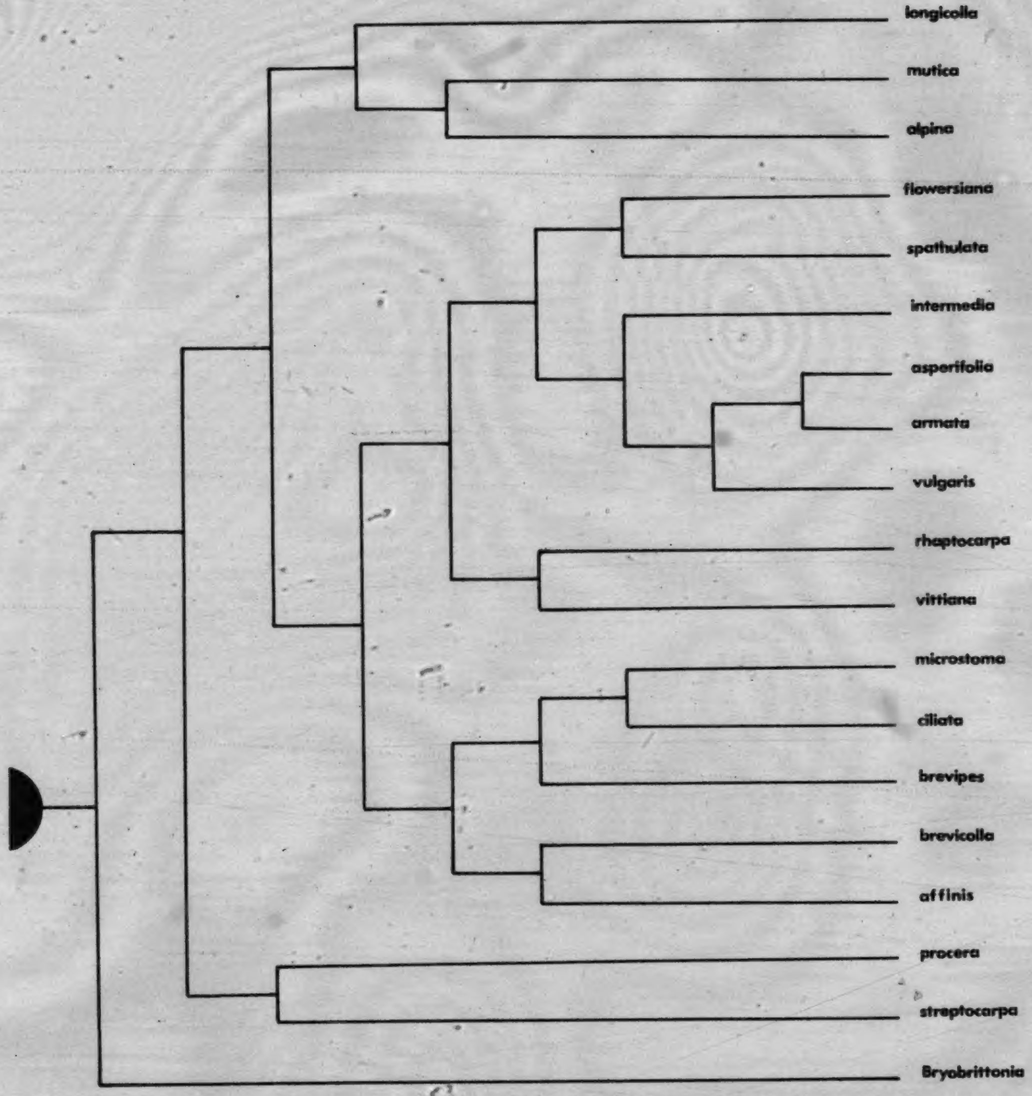

flowersiana
asperifolia
armata
intermedia
vulgaris
spathulata
rhaptocarpa
vittiana
brevipes
brevicolla
affinis
procera
streptocarpa
microstoma
ciliata
longicolla
alpina
mutica
2
4
6
8
10
12
14
16
18

Figure 299. Hennig Cladogram Illustrating the Inter-relationships Among Taxa in the Encalyptaceae as Determined by an Analysis of Trends in Character-state Evolution.


longicolla
mutica
alpina
flowersiana
spathulata
intermedia
asperifolia
armata
vulgaris
rhaptocarpa
vittiana
microstoma
ciliata
brevipes
brevicolla
affinis
procera
streptocarpa
Bryobrittonia

cylinder, whereas in many populations of *E. procera* there is a very slight, but distinct, contraction to the rostrum. In *E. streptocarpa* there are only one or two lacerations at the base of the cylinder, while there are five or six in many populations of *E. procera* and the base is divided into a number of fairly regular, broad segments. The very opaque calyptra of *E. streptocarpa* is quite dark and golden-brown in color. In contrast, that of *E. procera* is golden and slightly less opaque so that the capsule within is vaguely visible. In the Encalyptaceae, there is clearly a trend towards fusion of the double peristome, which ultimately results in a single peristome composed of several layers. Among the double peristomate species, *E. streptocarpa* has a peristome with both layers free and more-or-less unfused. In *E. procera*, the two layers are fused below and free only in the upper part. This would appear to be a slight derivation from the condition in *E. streptocarpa*. *Encalypta streptocarpa* is dioicous, while *E. procera* is autoicous. The spores of *E. procera* are twice the size of those of *E. streptocarpa* and therefore somewhat derived. It seems entirely possible that *E. procera* is an autopolyploid derivative of *E. streptocarpa*. There is one chromosome count of n=26 reported for *E. procera* (Steere 1954), but a count of *E. streptocarpa* has never been reported. As n=13 is the most frequent chromosome number reported in the Encalyptaceae (see Introduction), it will be interesting to see if this is not also the chromosome number of *E. streptocarpa*.

Encalypta streptocarpa is the only dioicous species of *Encalypta*. The change from the dioicous to the autoicous condition seems to be a significant one in the Musci that generally is not subject to reversal. Considering this and the fact that other plesiomorphous character-states that occur in *E. streptocarpa* are not to be found in any other species of *Encalypta*, it seems most plausible to hypothesize that all other species of *Encalypta* are derived from an ancestor very similar to *E. streptocarpa*, if not from *E. streptocarpa*.

(2) The *E. affinis*-*E. ciliata* Lineage. The species that are included in the *E. affinis*-*E. ciliata* lineage are *E. affinis*, *E. brevicolla*, *E. brevipes*, *E. ciliata*, *E. sibirica* and *E. microstoma* (Figs. 298-299). The word lineage is stressed because there are neither several, nor even one, character-states that are unique to these species as a whole. Indeed, the *E. affinis*-*E. ciliata* lineage is characterized by a diversity of character-states that reflect evolutionary divergence in a number of characters. Therefore, the species

that comprise this lineage are only linked on an individual basis, one to the next in step-wise fashion. The lineage is the composite result of the individual connections. The species with the most plesiomorphous character-states is E. affinis. Some of these suggest a link with E. procera or an ancestor similar to E. procera, but the slight modifications of most of these are also indicative of the directions of evolutionary change that gradually develop through the species in the E. affinis-E. ciliata line. In E. affinis the calyptra is golden and rather opaque, like that of E. procera. The rostrum of the calyptra is slightly, but distinctly, defined from the cylinder, perhaps a little more so than that of E. procera, and the rostrum is slightly longer than that of E. procera. The base of the cylinder is fringed in contrast with the lacerations that occur in E. procera. The peristome of E. affinis consists of single row of teeth, but these are each composed of two layers fused radially, so that it actually represents a double peristome. Therefore, this peristome could be quite readily derived from the partially fused, double peristome of E. procera. The peristome teeth are somewhat shorter in E. affinis. The narrow capsule mouth and rim are reminiscent of the same character-states in E. procera, but the capsules of E. affinis are smooth and not furrowed. The spores of E. affinis are approximately the same size as those of E. procera, but they are derived in other features. They are paraisopolar in shape, the surface sculpture consists of small or medium sized gemmae and they are brown, in contrast to those of E. procera that are isopolar, finely papillose and green. The seta of E. affinis is somewhat shorter than that of E. procera, but the leaves are much the same size. These trends of increasing definition and length of the calyptra rostrum, development of a fringe, reduction of the peristome in number of layers and length of the teeth, smooth capsules, development of polarity in the spores and shortening of the seta, begun in E. affinis are amplified in E. brevicolla. In addition, other trends, not yet apparent in E. affinis, begin with E. brevicolla.

Encalypta affinis is probably most closely related to E. brevicolla. This is particularly apparent in character-states of the calyptra. Both species have an opaque, golden calyptra with a long rostrum and the cylinder is lightly puckered. Also, there is a slight constriction at the base of the cylinder and below this there is a distinct, but rather irregular fringe. The trend towards increasing definition of the calyptra rostrum is apparent in E. brevicolla by comparison with E. affinis, and a new trend of reduction in total length of the calyptra is suggested by the slightly shorter calyptra of *E. brevicolla*. The basic structure of the peristome of *E. brevicolla* is very similar to that of *E. affinis*. It is a single peristome that is composed of four, fused layers of cell plates; however, the peristome of *E. brevicolla* is shorter than that of *E. affinis* and this is the completion of a trend in reduction of length of the peristome begun between *E. procera* and *E. affinis*. Certain trends are also apparent in the changes in the shape and structure of the capsule between *E. affinis* and *E. brevicolla*. The mouth of the capsule is broader in *E. brevicolla* and the rim is composed of more, better defined rows of cells. The outer surface of the capsule of *E. affinis* has a rather fragile appearance because the walls are only slightly thickened. With *E. brevicolla* there begins a trend towards a turgid-looking capsule with thickened exothecial cells. In *E. affinis*, as well as in *E. procera* and *E. streptocarpa*, the stomata are restricted to the base of the capsule. Therefore, this is regarded as the plesiomorphous condition. Derived from this is the condition of stomata scattered all over the surface of the capsule. This appears first in *E. brevicolla* in the *E. affinis-E. ciliata* lineage and also characterizes all the other species including *E. ciliata*, *E. brevipes* and *E. microstoma*. While the seta of *E. brevicolla* is as long as that of *E. affinis* in some populations, it is contrastingly short in others and this variability is the first indication of the general trend of decreasing length of the seta that continues through the rest of the *E. affinis-E. ciliata* lineage. The spores of *E. brevicolla* are more clearly polar (but still paraisopolar) than those of *E. affinis* and the ornamentation consists of verrucose projections. The spores of *E. brevicolla* are also apomorphous in that they are significantly larger than those of *E. affinis*. In features of the vegetative plants, *E. brevicolla* appears more closely related to *E. ciliata* than to *E. affinis*. *Encalypta affinis* is somewhat isolated from all species of *Encalypta* by the papillose walls of the basal cells, which must be considered an apomorphous character-state.

Encalypta brevicolla resembles *E. ciliata* in the broad marginal border at the base of the leaf and the coloration of the basal cells. There are also sporophytic features that suggest a close relationship between these two species. For example, the shape of the capsule with a broad constriction just below the mouth and the general turgid, smooth appearance of the surface of the capsule. Also, in both of these species there is a well-defined capsule rim of a number of rows of cells. The long rostrum of the calyptra in E. ciliata is a clear link with E. brevicolla, but the calyptra of E. ciliata is derived in several other features and reaches its ultimate apomorphous development in this species. The length of the calyptra is greatly reduced from that in E. brevicolla and there is a distinct ridge at the base of the cylinder above the precisely-defined fringe. This is clearly a derived condition by comparison to the slight constriction and rather irregular fringe of E. brevicolla. The reduction of the peristome is taken one step further in E. ciliata. In this species the peristome is single, but only consists of one layer of cell plates in contrast to the double-layered, single peristome of E. brevicolla. Similarly, the distinctly heteropolar spores of E. ciliata, with completely different ornamentation on the proximal and distal faces, clearly represent a derived condition by comparison to those of E. brevicolla. Reduction in the length of the seta is a continuing trend through E. ciliata. In E. ciliata, the seta never attains the lengths that it does in E. brevicolla.

Encalypta brevipes is gymnostomous, therefore, in this character-state it is more derived than either E. brevicolla or E. ciliata. Similarly, the seta of E. brevipes is much shorter than that of E. brevicolla or E. ciliata and represents the ultimate derivation of this character-state in the Encalyptaceae. However, there are characteristics of the plants of E. brevipes that are suggestive of both of these species. The smooth, turgid-looking capsules that are quite broadly constricted below the mouth have a well-defined, distinct rim of numerous rows of cells. The stomata are scattered over the surface of the capsule as they are in both E. brevicolla and E. ciliata. The slightly puckered calyptra with a slight constriction at the base above the rather irregular fringe is more similar to that of E. brevicolla. The very short, stubby rostrum and the short overall length of the calyptra are clearly derived features in comparison with either E. brevicolla or E. ciliata. Encalypta brevipes also resembles E. brevicolla in the dark-green and blackish coloration of the hair-pointed leaves. The spores of E. brevipes are indistinctly polarized in shape, but the sculpture is quite different from that of E. brevicolla. The spores of E. brevipes are less derived than those of E. ciliata, and there is no evidence that this character is subject to character-state reversal, but E. brevipes is more derived than either E. ciliata or E. brevicolla in the lack of a peristome, and the short calyptra and rostrum. Therefore, it seems most plausible to consider that E. brevipes is derived from a now-extinct ancestor between E. ciliata and E. brevicolla.

Based on structural similarities, the relationship between *E. ciliata*, and *E. microstoma* and *E. sibirica* appears to be closer than that between any other species in the *E. affinis–E. ciliata* lineage. Rather than enumerating the character-states that *E. ciliata*, and *E. sibirica* and *E. microstoma* have in common, it is perhaps more to the point to note that they can be differentiated only by slight differences in the shape of the calyptra, the lack of a peristome in *E. microstoma* and a slightly different shape in the upper part of the capsule, and differences in the apex and marginal structure of the leaves. The calyptra is slightly shorter in *E. microstoma* than in *E. ciliata*, which is a continuation of this reductive trend. However, the rostrum is slightly less distinctly defined in *E. microstoma* than it is in *E. ciliata* and this then appears to be a reversal in the trend of increasing definition of the rostrum seen through *E. affinis*, *E. brevicolla* and *E. ciliata*. Also, the ridge at the base of the cylinder is not as distinctly defined in *E. microstoma* as it is in *E. ciliata* and this also appears to be a slight reversal. The lack of a peristome in *E. microstoma* is the ultimate reduction of the peristome and represents the end-point in this particular trend. The seta of *E. microstoma* is consistently shorter than that in most populations of *E. ciliata*. Again, this represents the end-point of the reduction series in seta length.

In summary, the evolutionary trends apparent in the gradual modification of character-states between the different species in the *E. affinis–E. ciliata* lineage contribute to the overall impression of contiguity among these species. The major trends include the reduction in the length of the calyptra, and increasing definition of the rostrum and fringe, which are most apparent between *E. affinis*, *E. brevicolla* and *E. ciliata*. Also, the reduction of the peristome from one that is single, but consists of two layers, in *E. affinis* and *E. brevicolla*, through one that is single and consists of one layer in *E. ciliata* to the complete lack of a peristome in *E. brevipes*, *E. sibirica* and *E. microstoma*. The increase in polarity of spores is most evident between *E. brevicolla* and *E. ciliata*. The trend towards reduction in seta length is most sharply defined between *E. brevicolla* and *E. ciliata*, and then between *E. ciliata* and *E. microstoma–E. brevipes*.

(3) The *E. rhaptocarpa–E. vulgaris* Complex. The species included in this complex are *E. rhaptocarpa*, *E. vittiana*, *E. spathulata*, *E. flowersiana*, *E. intermedia*, *E. vulgaris*, *E. asperifolia*, *E. armata* and *E. armata* (Figs. 298–299). In contrast to the *E. affinis–E. ciliata* lineage where there is no character-state that unifies the group as a whole, the species

in the *E. rhaptocarpa-E. vulgaris* complex are all characterized by distinctly heteropolar spores with large, hollow verrucose protuberances on the distal surface. That such a large group of species should all have the same spore-type is noteworthy by comparison to other species of *Encalypta*, most of which have unique spore ornamentation. As well, many of the species in the *E. rhaptocarpa-E. vulgaris* complex are difficult to differentiate, at least in some populations, because of structural intergradation. Therefore, these species are not as clearly defined as are other species of *Encalypta* and this leads me to believe that this group is relatively young and actively evolving. The fact that a number of species in this complex are narrow endemics also supports such a point-of-view. For these reasons the word "complex" is considered more appropriate in this instance than "group" or "lineage".

While the *E. rhaptocarpa-E. vulgaris* complex forms a very natural group, it is difficult to discern to which other species of *Encalypta* they are most closely related. The species with the most plesiomorphous character-states is *E. rhaptocarpa*. It has a single peristome composed of two fused layers of cell plates, similar to that of *E. ciliata*. Also, the seta and leaves are approximately the same size as those of *E. ciliata*; therefore, the plants are of similar size. Spores of *E. rhaptocarpa* are heteropolar as are those of *E. ciliata*. These features indicate that in several unrelated characters, *E. rhaptocarpa* is at an evolutionary level parallel to *E. ciliata*. However, neither the vegetative plants nor the sporophytes, except for the peristome structure, of *E. rhaptocarpa* show much, if any, resemblance to *E. ciliata*. The ornamentation of the spores is quite different. In this respect, the spores of *E. rhaptocarpa* are rather similar to those of *E. brevicolla*. *Encalypta brevicolla* is also characterized by spores with verrucose protuberances on the distal surface; however, in *E. brevicolla* these do not appear to be hollow as they are in the *E. rhaptocarpa-E. vulgaris* complex. The form of the calyptra in *E. rhaptocarpa* is basically quite different from that of *E. brevicolla*. The rostrum is shorter and the calyptra as a whole is shorter. As well, there is no suggestion of a fringe at the base of the cylinder. However, this calyptra-type that occurs in *E. rhaptocarpa* must be considered derived because the rostrum is well-defined and there is no segmentation of the base of the cylinder as is found in the basal group of species, for example, *E. procera*. In spite of the differences between the calyptra of *E. rhaptocarpa* and *E. brevicolla*, there is something inexplicable in the coloration and overall appearance that suggests it would be possible to derive such a calyptra as that of E. rhaptocarpa from E. brevicolla. Encalypta rhaptocarpa seems to be at approximately the same evolutionary level as E. ciliata, but the only resemblance with that species is in the peristome-type. The spore structure of E. rhaptocarpa suggests a possible relationship with E. brevicolla, but E. rhaptocarpa has more apomorphous character-states than E. brevicolla. Therefore, I have concluded that the most plausible ancestral type for E. rhaptocarpa would be a now-extinct species of Encalypta between E. brevicolla and E. ciliata (Figs. 298-299).

Encalypta rhaptocarpa and E. vittiana are the only species in the E. rhaptocarpa-E. vulgaris complex with a well-developed, single peristome. That is, the teeth are dark-orange. The relationship between E. rhaptocarpa and E. vittiana is at least as close as that between E. ciliata and E. microstoma. Encalypta rhaptocarpa and E. vittiana can be differentiated only by character-states of the calyptra. The most obvious of these is the well-developed fringe at the base of the cylinder in E. vittiana. If E. vittiana is derived from E. rhaptocarpa, then the fringe must have arisen secondarily as the base of the cylinder is erose in E. rhaptocarpa, as noted above. There are other species in the E. rhaptocarpa-E. vulgaris complex, for example E. spathulata, E. flowersiana, E. asperifolia and E. armata, that have a more-or-less well-developed fringe that appears to have arisen secondarily. All of these species lack a peristome and are considered to be ultimately derived from a species with a single peristome. As noted above, the only two species in the group with this character-state are E. rhaptocarpa and E. vittiana; however, E. vittiana is so restricted in its pattern of distribution that it is more likely that E. rhaptocarpa, which has a very widespread range, is the progenitor. It is also possible that the common ancestor of E. ciliata and the E. rhaptocarpa-E. vulgaris complex had a well-developed calyptra fringe and that E. vittiana is more closely related to this ancestral type than is E. rhaptocarpa. In this instance, E. rhaptocarpa must be considered to be derived from E. vittiana.

The evolutionary trend towards the gymnostomous condition is particularly evident in the E. rhaptocarpa-E. vulgaris complex not only interspecifically, but also intraspecifically. For example, while E. rhaptocarpa is generally characterized by the presence of a well-developed peristome, as described above, there are many populations of *E. rhaptocarpa* with a more-or-less poorly developed peristome. In such instances, the teeth are pale-orange, but otherwise undifferentiated from those that are found in a well-developed peristome, or they are hyaline, very sparsely papillose and much shorter than those in a well-developed peristome. In a few populations of *E. rhaptocarpa*, the peristome is completely lacking. Other examples of the evolutionary trend towards loss of the peristome are to be found in two species generally considered to be gymnostomous, *E. vulgaris* and *E. spathulata*. While the majority of populations of both of these species do lack a peristome, there are a few in which there is a vestigial peristome at the mouth of some of the capsules. The species that never show any suggestion of a peristome, *E. flowersiana*, *E. asperifolia*, *E. armata* and *E. intermedia s. str.* can probably be considered the most derived in the *E. rhaptocarpa*–*E. vulgaris* complex. Some of these have unique features that support such an assumption. For example, the spores of *E. flowersiana* always have most of the verrucose projections on the distal surface fused to form vermiform protuberances, and in *E. armata* there are very long, spinose projections on the back of the costa and on the rostrum of the calyptra that occur in no other species of *Encalypta*.

Two or three other evolutionary trends are also apparent in the *E. rhaptocarpa*–*E. vulgaris* complex. Decrease in the length of the seta correlates quite closely with loss of the peristome. *Encalypta rhaptocarpa* has a seta of moderate length, while all other species, *E. vittiana*, *E. vulgaris*, *E. spathulata*, *E. flowersiana*, *E. asperifolia*, *E. armata* and *E. intermedia*, all have a short or very short seta. There is also the trend towards decreasing length of the calyptra, which is particularly apparent in *E. spathulata*, *E. flowersiana* and *E. intermedia*. Among the species in the *E. rhaptocarpa*–*E. vulgaris* complex, most are characterized by a moderately opaque calyptra; however, the derived condition of a very transluscent, pale calyptra is found in both *E. spathulata* and *E. flowersiana*.

As noted above, the species in the *E. rhaptocarpa*–*E. vulgaris* complex are at times difficult to differentiate from one another. The structural similarities and the lack of a peristome in most species also make it problematical to determine the exact nature of the inter-relationships among them. The core species are considered to be *E. rhaptocarpa* and *E. vulgaris* because *E. rhaptocarpa* is the only species with a peristome (aside from *E. vittiana*) and *E. vulgaris* seems to be very closely related in that some populations of these two species are virtually impossible to differentiate. Also, these two species are the most widespread of any of the species in the *E. rhaptocarpa–E. vulgaris* complex. Close relationships between other species are also evident. For example, *E. flowersiana* differs from *E. spathulata* only in spore structure and the structure of the leaf apex. The different spore structure of *E. flowersiana* suggests that it is derived from *E. spathulata* as this feature occurs nowhere else in the *E. rhaptocarpa–E. vulgaris* complex. Also, the structure of the calyptra of *E. armata* is virtually identical to that of *E. asperifolia*; therefore, it is reasonable to consider that these two species are very closely related. In this instance, the spinose calyptra and leaves of *E. armata* are a good indication that this is the more derived taxon. However, the problem of exactly how *E. spathulata*, *E. asperifolia* and another gymnostomous species, *E. intermedia*, relate to *E. rhaptocarpa* and *E. vulgaris* is difficult to clarify. All three of these species have structural features, some of which are more like those of *E. rhaptocarpa*, for example the more-or-less ribbed capsules, and others that are more suggestive of *E. vulgaris*, for example, the lack of a peristome and a very prominent, shiny costa. The relationships of these taxa back to hypothetical ancestors between *E. rhaptocarpa* and *E. vulgaris* are indicated with the realization that there probably cannot be an entirely satisfactory representation on the basis of the data presently available.

(4) Species with Ambiguous Affinities. *Encalypta longicolla*, *E. alpina* and *E. mutica* are treated as a unit because there are some vague indications that they may be more closely related to one another than to other species of *Encalypta*. However, the inter-relationships among these species are indicated with some hesitancy as are the more general relationships of the group as a whole (Figs. 298–299).

Encalypta longicolla is the only one of these species with a peristome. It is single, but consists of two fused layers; therefore, it is of the same type that is found in *E. affinis* and *E. brevicolla*. In some other character-states, *E. longicolla* also seems to be at about the same evolutionary level as *E. affinis* and *E. brevicolla*. For example, the rostrum of the calyptra is well-defined as in *E. brevicolla* and there is a fairly well-developed fringe at the base of the cylinder, although the structure of this fringe is quite different from that in *E. affinis* and *E. brevicolla*. The calyptra is quite dark in color and rather opaque. Spores of *E. longicolla*, like those of *E. affinis* and *E. brevicolla* are paraisopolar.

However, in several features, *E. longicolla* seems strikingly derived. For example, the spores are much larger and the leaves are much narrower than those of any other species of *Encalypta*. Also, the seta is shorter than that of *E. affinis* and *E. brevicolla*. There are no characteristics, other than the basic structure of the peristome, that suggest a relationship between *E. longicolla* and the species in the *E. affinis-E. ciliata* lineage. It seems entirely possible that the trend towards fusion of the double peristome may have taken place in more than one line. Coloration of the vegetative plants, seta, peristome and calyptra of *E. longicolla* all suggest a derivation from *E. procera* or a closely related species.

Encalypta alpina is another species like *E. longicolla* that is derived in some character-states while retaining others that are plesiomorphous. Character-states that are more plesiomorphous include the paraisopolar spores, the moderately long seta and the dark calyptra with the base of the cylinder lacerate. In all of these features, except the base of the calyptra, *E. alpina* is only slightly more derived than *E. procera* and the lacerate calyptra is also characteristic of *E. procera*. The only highly derived feature of *E. alpina* is the lack of a peristome. Also, the narrowly acute leaves that occur in no other species of *Encalypta* probably also represent a derived condition. Overall, most character-states of *E. alpina*, including the lacerate calyptra, the color of the seta, capsules and vegetative plants, suggest a distant relationship with *E. procera* or a closely related species. The shape and color of the calyptra, particularly the well-defined, moderately long rostrum and the overall shininess of the calyptra, also suggest that *E. alpina* may also be distantly related to *E. longicolla*. Similarities in habitat preferences of these two species add further weight to such a suggestion. *Encalypta alpina* grows in the most mesic habitats of any species of *Encalypta, but among the rest, E. longicolla* frequently occurs in habitats almost as mesic as those characteristic of *E. alpina*.

In most character-states, *E. mutica* is derived. The calyptra is exceptionally short with a very short, well-defined rostrum and well-developed fringe. Also, the calyptra is very pale in color and almost transparent. The capsule is gymnostomous, and both the seta and the leaves are very short. Overall, the plants are the smallest of any species of *Encalypta*. When Hagen (1899) described *E. mutica*, he stated that it is closely related to *E. vulgaris*. Later, Tuomikoski (1935) suggested that plants of *E. mutica* that he had examined were reminiscent of a small form of *E. rhaptocarpa*-*E. vulgaris*, and concluded that *E. mutica* is closely related to these two species. Most recently, Horton and Murray (1976) considered the relationships of *E. mutica* as might be inferred on the basis of spore structure. They concluded that the "...highly ornamented 'cauliflower' papillae of *E. mutica*..." are most reminiscent of a group of species including *E. alpina*, *E. ciliata*, *E. rhaptocarpa* and *E. vulgaris*, as delimited by Vitt and Hamilton (1974).

In the Encalyptaceae, peristome and spore structure are considered to be fundamentally reliable features for determining evolutionary relationships among the different species as discussed above. Character-states of capsules, setae, leaves and cells may also indicate relationship in some instances, but they are less reliable and when these are at variance with evidence from peristome and spore morphology, I believe that the latter two characters should be given greater weight. The similarities between *E. mutica* and *E. vulgaris* and some forms of *E. rhaptocarpa* including the small size of the plants, the lack of a peristome, capsule shape and the muticous leaves could be cited as evidence suggesting a relationship between these species as Tuomikoski (1935) and Hagen (1899) did with respect to *E. vulgaris*. However, as Tuomikoski noted, the spores of *E. mutica* are not at all like those of either *E. rhaptocarpa* or *E. vulgaris*. Spore structure is the one feature in which *E. mutica* is not particularly derived. The spores are paraisopolar and there are small, irregular gemmae over the entire surface. Therefore, I suspect that the other structural similarities between *E. mutica*, and *E. rhaptocarpa* and *E. vulgaris* are superficial and probably represent convergent evolution. The relationship of these two species to *E. mutica* is probably a distant one. The species of *Encalypta* with spore ornamentation very similar to that of *E. mutica* is *E. alpina*. In *E. alpina*, the gemmae are very small, but similarly irregular to those of *E. mutica*. Other structural similarities between these two species have proven to be elusive. The only other feature that I have been able to identify is that in some populations of *E. alpina* the old capsules are virtually identical in structure to those of *E. mutica*. As *E. alpina* has more plesiomorphous character-states than *E. mutica*, it would seem more likely that *E. mutica* is derived from *E. alpina* or a closely related species.

As noted in the Introduction, the importance of habitat in defining any group of plant species is not to be underestimated and is here considered to be of equivalent importance to many significant structural features. In general, species of Encalypta are commonly associated with mountainous terrain where they occur on rock outcrops and disturbed soil throughout the montane, subalpine and alpine zones. These are relatively xerophytic, exposed habitats characterized by light winter snow cover and early spring melt; however, the microhabitats where the plants grow, on the edge of solifluction terracettes, crevices of rock outcrops or depressions in tundra, are quite protected and probably mesophytic. Some species of Encalypta occur in similar habitats in the Arctic, and a few species are to be found in non-montane habitats of the subarctic, boreal and prairie ecosystems. In such areas, the populations are most frequently associated with rock outcrops along river banks. The monotypic genus Bryobrittonia is generally found on exposed alluvial soil along rivers, often very close to the water level. Populations rarely occur in alpine tundra and crevices of rock outcrops.

Within this general framework, there are distinctions between individual species. The most obvious of these is the correlation between differences in substrate type and the occurrence of species of Encalypta. A comparison of substrate preferences of the four groups of species of Encalypta, outlined above, reveals correlations and apparent evolutionary trends. Soil samples have been collected with species of Encalyptaceae throughout their ranges in North America. The data resulting from analyses for pH, and exchangeable Ca^{++} and Mg^{++} concentrations are presented in Figs. 300, 301, 302 and Table 9, with the order of species following that established on the basis of pH (Fig. 300). In the E. procera-E. streptocarpa group, E. procera shows a rather marked preference for substrates with a relatively high pH, but populations also occur on substrates with a slightly subneutral pH. The range is from 6.5 to 7.8 with a mean of 7.3 (Fig. 300). From all accounts in the literature and from my own experience, this applies equally to E. streptocarpa. Similarly, E. procera is found on substrates with both a relatively high Ca^{++} and Mg^{++} content (Figs. 301-302, Table 9).

With respect to the species in the E. affinis-E. ciliata lineage, there is an evolutionary trend from substrates with a relatively high pH to those with a very low pH and this trend is paralleled in Ca^{++} and Mg^{++} concentrations (with the exception of E. affinis). Encalypta affinis has rather broad tolerances of substrates with a pH as low as 5.9 and as high as 7.3; however, the mean is slightly acidic at 6.7. The range is similarly

Figure 300. pH of Substrate Samples Collected With Populations of Encalyptaceae in Western North America.

Horizontal line indicates the range; vertical line indicates the mean; white bar indicates one and one-half standard deviations on either side of the mean; and black bar indicates two standard errors on either side of the mean.

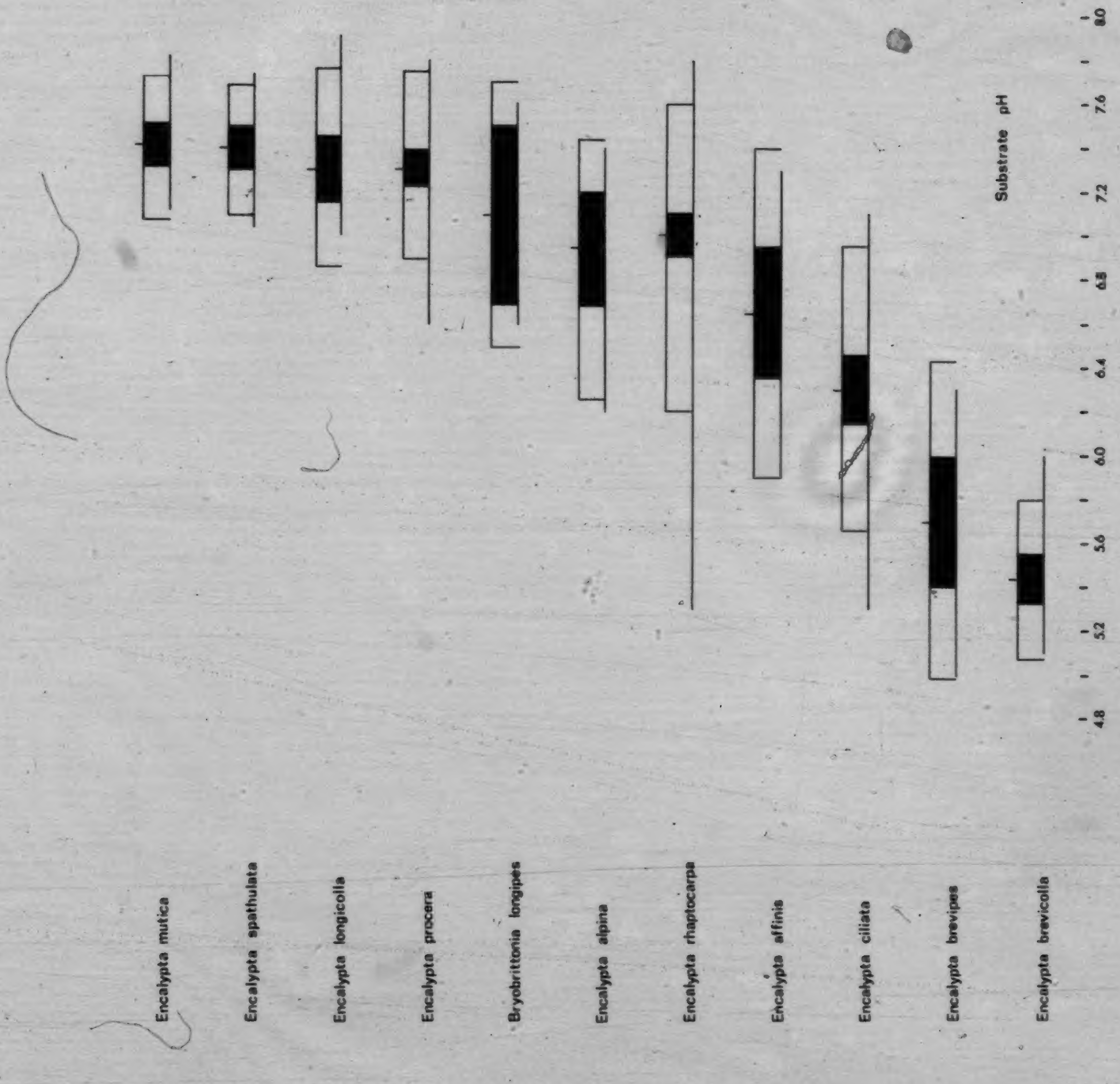

Encalypta mutica
Encalypta spathulata
Encalypta longicolla
Encalypta procera
Bryobrittonia longipes
Encalypta alpina
Encalypta rhaptocarpa
Encalypta affinis
Encalypta ciliata
Encalypta brevipes
Encalypta brevicolla
Substrate pH
4.8
5.2
5.6
6.0
6.4
6.8
7.2
7.6
8.0

Figure 301. Ca^{++} Concentration of Substrate Samples Collected With Populations of Encalyptaceae in Western North America.

Vertical line indicates the mean; horizontal line indicates one and one-half standard deviations on either side of the mean; and black bar indicates two standard errors on either side of the mean.

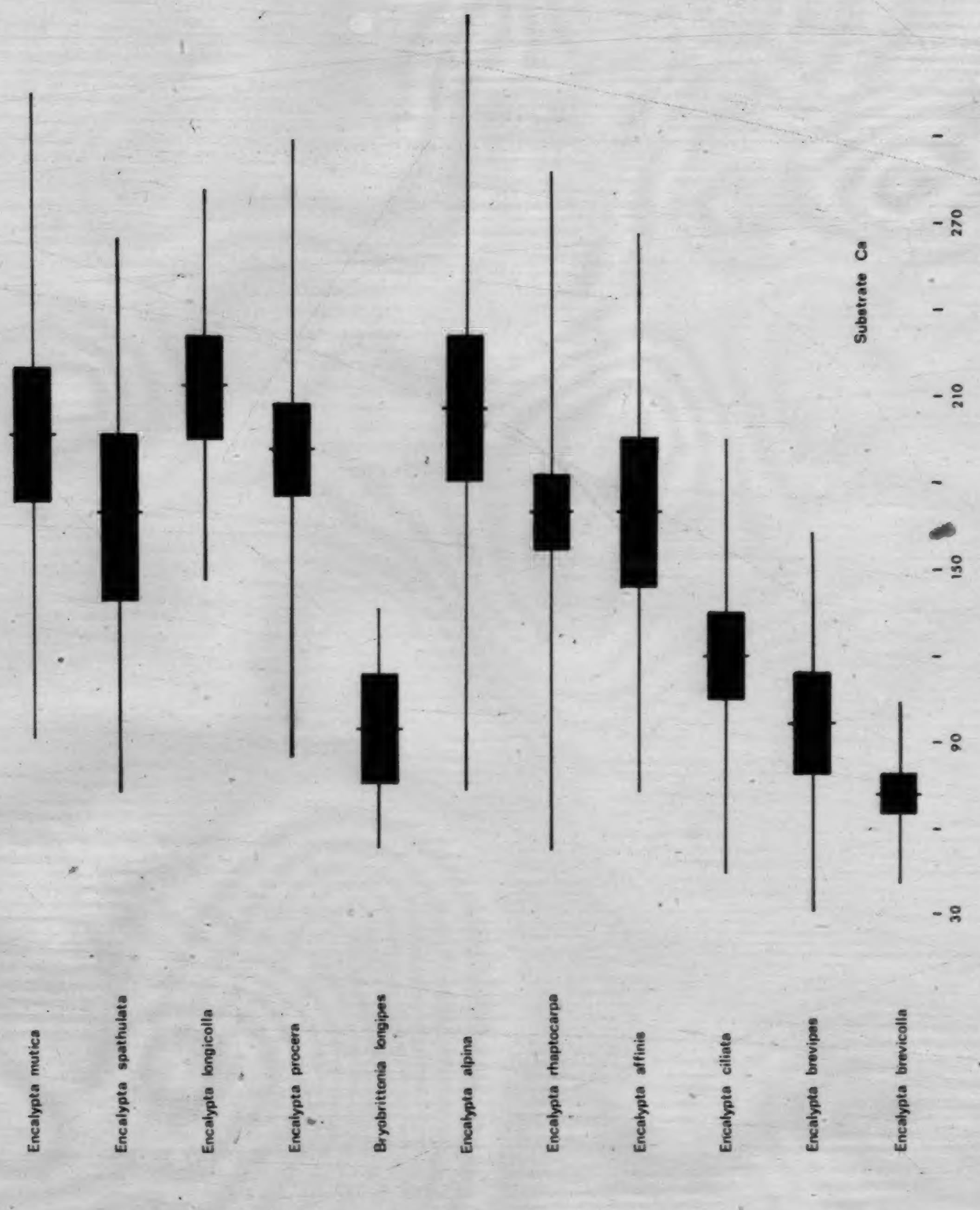

Encalypta mutica
Encalypta spathulata
Encalypta longicolla
Encalypta procera
Bryobrittonia longipes
Encalypta alpina
Encalypta rhaptocarpa
Encalypta affinis
Encalypta ciliata
Encalypta brevipes
Encalypta brevicolla
Substrate Ca
30
90
150
210
270

Figure 302. Mg^{++} Concentration of Substrate Samples Collected With Populations of Encalyptaceae in Western North America.

Vertical line indicates the mean; horizontal line indicates one and one-half standard deviations on either side of the mean; and black bar indicates two standard errors on either side of the mean.

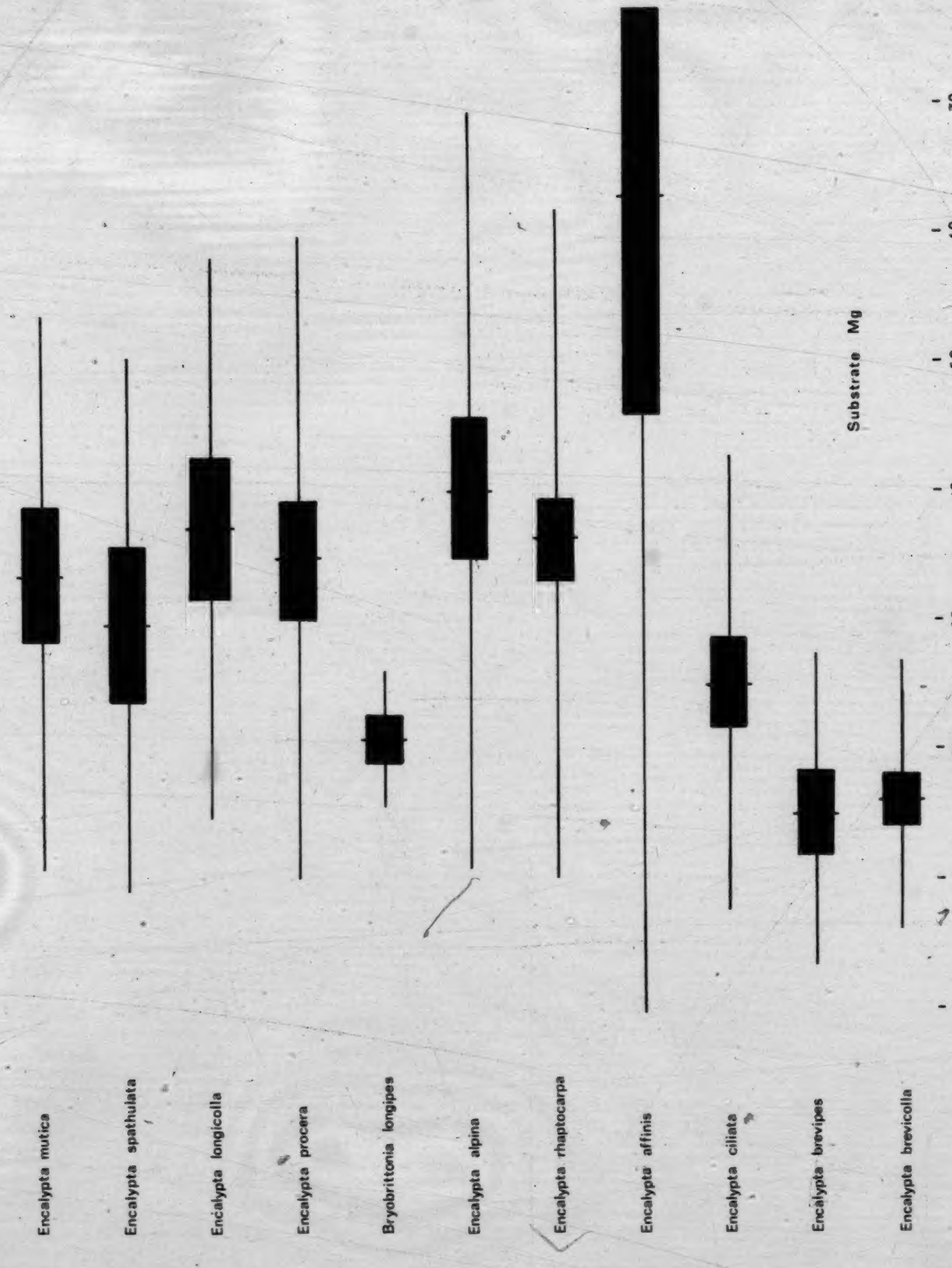

Encalypta mutica
Encalypta spathulata
Encalypta longicolla
Encalypta procera
Bryobrittonia longipes
Encalypta alpina
Encalypta rhaptocarpa
Encalypta affinis
Encalypta ciliata
Encalypta brevipes
Encalypta brevicolla
Substrate Mg
0
10
20
30
40
50
60
70

Table 9. EXCHANGEABLE CA^{++} AND MG^{++} IN SOIL SAMPLES COLLECTED IN WESTERN NORTH AMERICA WITH SPECIES OF ENCALYPTACEAE. Total number of samples = 280

	Ca^{++}				Mg^{++}			
	Mean	±s.d.	n	Range	Mean	±s.d.	n	Range
E. mutica	197	106	21	45-495	33	21	21	6-90
E. spathulata	169	96	11	25-440	30	21	11	8-55
E. longicolla	214	68	14	70-360	37	21	14	3-71
E. procera	192	107	46	40-441	35	25	46	5-168
B. longipes	95	42	5	45-155	21	5	5	17-30
E. alpina	206	134	28	35-557	40	29	27	4-90
E. rhaptocarpa	170	118	82	45-540	36	26	81	4-172
E. affinis	170	98	14	45-430	63	64	12	8-192
E. ciliata	120	76	27	4-294	25	18	28	1-66
E. brevipes	97	66	13	45-285	15	12	13	3-41
E. brevicolla	72	32	19	29-145	16	10	19	5-45

quite broad with respect to Ca^{++} concentration of the substrate and the mean is slightly lower than most species of *Encalypta* (besides those in the *E. affinis-E. ciliata* lineage). However, the results of the analyses for Mg^{++} concentration reveal that *E. affinis* has an extraordinarily broad range of tolerance for this element and, relative to other Encalyptaceae, a preference for exceptionally high concentrations (Fig. 302, Table 9). The general trend towards lower pH, and Ca^{++} and Mg^{++} concentrations is evident in *E. ciliata* by comparison to *E. affinis*. In *E. ciliata* the range in pH is from 5.3 to 7.1 with a mean of 6.3 (Fig. 300) and the Ca^{++} and Mg^{++} concentrations are correspondingly lower than most other species of *Encalypta* (except those in this lineage) (Figs. 301-302, Table 9). The ultimate expression of this trend into acidic habitats is realized in *E. brevipes* and *E. brevicolla*. Both species are restricted to substrates with a pH well below neutral, and low concentrations of Ca^{++} and Mg^{++}. *Encalypta brevipes* occurs on substrates with a range in pH of 5.0 to 6.3 and a mean of 5.7 (Fig. 300), while *E. brevicolla* is found over a range of 5.1 to 6.0 with a slightly lower mean of 5.4 (Fig. 300). The Ca^{++} and Mg^{++} concentrations for these two species are lower than those for any other species of *Encalypta* (Figs. 301-302, Table 9).

Of the species in the *E. rhaptocarpa-E. vulgaris* complex, I have complete data available for *E. rhaptocarpa* and *E. spathulata*; however, on the basis of limited field experience and data, it is possible to make inferences about the preferences of several other species. In this complex, there appears to be a trend towards highly calcareous habitats. The least derived species in this group, *E. rhaptocarpa*, appears to have broader tolerances with respect to substate pH than any other species of *Encalypta*. It has been found on substrates ranging from 5.3 to 7.8, but there is a slight preference for slightly higher pH with a mean of 7.0 (Fig. 300). It is found over a rather broad range of Ca^{++} and Mg^{++} concentrations as well, and here too, the preference is for substrates with slightly higher concentrations (Figs. 301-302, Table 9). However, *E. spathulata* is highly restricted and occurs only on substrates with a high pH. The range is from 7.0 to 7.8 with a mean of 7.4 (Fig. 300). This preference is not as evident on the basis of Ca^{++} and Mg^{++} concentrations (Figs. 301-302, Table 9). From the data available on the nature of the substrate at the localities where *E. flowersiana* has been collected (see Habitat under *E. flowersiana*), it also appears to be restricted to substates with a high pH. *Encalypta* *intermedia* has been collected only on highly calcareous substrates (pH 7.5, Ca^{++} 203, Mg^{++} 43, n=27), generally limestone. My experience with *E. asperifolia* is limited, but this species was found only on limestone in Peru (pH 7.1, Ca^{++} 236, n=7); therefore, it may well be that this narrowly distributed species is restricted to substrates with a high pH. Among the taxa in the *E. rhaptocarpa*–*E. vulgaris* complex about which any statement can be made with respect to their substrate preferences, the species considered derived on the basis of structure appear to be more restricted to highly calcareous substrates.

In the *E. alpina*–*E. longicolla* group, the trend also seems to be into highly calcareous habitats. Just as there are a number of structural features of *E. alpina* that are less derived than the gymnostomous condition would suggest, it seems less derived in substrate preferences. It has rather broad tolerances of substrate pH from 6.2 to 7.4, but the mean is 7.0 (Fig. 300). It has similarly broad tolerances of Ca^{++} and Mg^{++} concentrations, although here too the mean is higher than is found in many species of *Encalypta* (Figs. 301–302, Table 9). Just as *E. longicolla* appears anomalously derived in some character-states in comparison with the peristome structure, it seems highly derived in substrate preferences. It is restricted to substrates with a high pH, ranging from 6.9 to 7.9 with a mean of 7.3 (Fig. 300). Concentrations of Ca^{++} and Mg^{++} are correspondingly high (Figs. 301–302, Table 9). On the basis of habitat preferences, *E. mutica* appears to be derived as it does on the basis of structure. It is restricted to highly calcareous habitats with a pH of 7.1 to 7.8 and a mean of 7.4 (Fig. 300). Concentrations of Ca^{++} and Mg^{++} are in general correspondingly high (Figs. 301–302, Table 9). Therefore, the trend in this group of species seems to have been for the structurally more highly evolved species to be restricted to highly calcareous habitats.

Based on the above data, it can be inferred that the ancestral type in the Encalyptaceae probably occurred more frequently on slightly calcareous substrates with a higher pH, although it had a slight tolerance for subneutral pH. This type is presently exemplified by *E. procera* and *E. streptocarpa*. A derived condition within the Encalyptaceae is considered to be found in those species with a relatively broad tolerance with respect to substrate pH. This includes such species as *E. affinis*, *E. alpina*, *E. ciliata* and *E. rhaptocarpa*, all of which occur on both substrates that are more-or-less acidic or calcareous, although all of these species show a marked preference for one substrate-type or the other. The most derived conditions are considered to be represented by two evolutionary trends. Some species, for example, E. brevipes and E. brevicolla have evolved into highly acidic habitats and are restricted to such habitats. The fact that E. brevicolla has a highly derived habitat-preference shows that the evolution of this feature has not necessarily correlated with the rate of evolution of structural features. Another trend is apparent in both the E. rhaptocarpa-E. vulgaris complex and the E. alpina-E. longicolla group. This is the restriction of more highly derived species to highly calcareous substrates.

Species of Encalyptaceae grow in montane and arctic habitats typical of many other species of mosses. On the basis of extensive field work in western North America, I believe that the three substrate preferences demonstrated by species of Encalypta are representative of the fundamental preferences of arctic-montane species of mosses in general. That is, some species are restricted to highly acidic substrates, while others are restricted to highly calcareous substrates. Most have broad tolerances of both acidic and calcareous substrates, but show a marked preference for one substrate-type or the other.

It should be apparent from the foregoing discussions of structural features and substrate preferences that there are at least three, and possibly a fourth, natural clusters of species within the Encalyptaceae. One of these, the E. rhaptocarpa-E. vulgaris complex, is readily defined by the spore structure and a second, the E. procera-E. streptocarpa group, can be differentiated by the double peristome. The third group, the E. affinis-E. ciliata lineage, is difficult to define because there is no all-encompassing character-state with which to recognize the group as a unit. There is the same problem with the fourth group, the E. longicolla-E. alpina group. Furthermore, while I feel absolutely confident that the first three groups are truly natural assemblages, I am uncertain with respect to this last group. Therefore, in view of the difficulty of defining two of these groups and considering that one grouping may not be the best representation of the natural relationships, I am hesitant to recognize subgenera or sections within the genus Encalypta. However, if they are to be recognized, the correct names at the sectional level and the included species would be as follows:

Sect. **_Streptotheca_** (Kindb.) Broth.,
Nat. Pfl. 1(3): 438. 1902.

Basionym: Subg. *Streptotheca* Kindb., Eur. N. Am. Bryin. 2: 293. 1897. Lectotype: *E. contorta* Hoppe *ex* Lindb. (=*E. streptocarpa*).

E. procera

Sect. **_Pyromitrium_** Wallr. *ex* Hampe,
Linnaea 513. 1872.

Type: **_E. alpina_** Smith.

E. longicolla, E. mutica.

Sect. **_Psilotheca_** C. Müll.,
Syn. 1: 513. 1849.

Lectotype: **_E. ciliata_** Hedw.

E. affinis, E. brevicolla, E. brevipes, E. microstoma, E. sibirica

Sect. **_Rhabdotheca_** C. Müll.,
Syn. 1: 519. 1849.

Lectotype: **_E. rhaptocarpa_** Schwaegr.

E. armata, E. asperifolia, E. flowersiana, E. intermedia, E. spathulata, E. vittiana, E. vulgaris.

Relationships of *Bryobrittonia*

On the basis of a number of sporophytic features, or gametophytic features that are closely associated with the sporophyte, it is obvious that *Bryobrittonia* is very closely related to *E. streptocarpa* and *E. procera*. The shape and color of the calyptra, the double peristome, the furrowed capsule with a narrow, irregular rim, the small, finely papillose spores that are apolar, and the long seta, among others; all are characteristic of *E. streptocarpa* and *E. procera*, as well as of *Bryobrittonia*. As well, *Bryobrittonia* and *E. streptocarpa* are the only species in the Encalyptaceae that are dioicous. There can be no doubt that *Bryobrittonia* belongs in this family with the species of *Encalypta*. However, *Bryobrittonia* is strikingly differentiated from *E. streptocarpa* and *E. procera*, indeed all species of *Encalypta*, by the gametophytic character-states of smooth upper laminal cell walls, thin basal cell walls, and crenulate leaf margins. In contrast, species of *Encalypta* are all characterized by papillose upper laminal cell walls, the transverse walls of the basal cells thickened and entire leaf margins. These differences definitely warrant recognition of *Bryobrittonia* as a genus distinct from *Encalypta*. This is also a good example of the lack of synchrony in the evolutionary development of the sporophyte and gametophyte that characterizes many groups in the Musci.

Inter-relationships of the Encalyptaceae

In order to establish the natural affinities between groups of mosses above the level of genus, several fundamental characters are generally useful. These include the growth habit, cell structure of the leaves and the peristome-type. In addition, particularly distinctive features of a family, for example, the calyptra in the Encalyptaceae, also prove important in some instances.

The acrocarpous growth habit of the Encalyptaceae is a fundamental characteristic that differentiates the family from all the pleurocarpous families of Bryidae, that is, the Hypnaceae, Brachytheciaceae, Leucodontaceae, Thuidiaceae, and others. A particularly striking feature of the Encalyptaceae, that has proven to be of ultimate significance in establishing the familial concept, is the mitrate calyptra, to which the family owes its name (Schreber 1791). Mitrate calyptrae are of sporadic occurrence in such other acrocarpous families as the Orthotrichaceae, the Pottiaceae, the Dicranaceae, the Funariaceae and the Grimmiaceae, but the calyptrae that occur in most of these are considerably shorter than that which characterizes the Encalyptaceae. The calyptra-type that occurs in the orthotrichaceous genus *Schlotheimia* most closely approaches the basic shape of the calyptra in the Encalyptaceae. In all species of *Schlotheimia*, the calyptra is longer than the capsule and the base is fringed giving it an appearance very reminiscent of *E. ciliata* or *E. mutica*; however, the rostrum is never distinctly differentiated from the cylinder in species of *Schlotheimia*, as it is in many species of Encalypta. In a survey of the different calyptra-types that occur in the Musci, Janzen (1916) demonstrated that it is not the shape of the calyptra that is of fundamental importance in determining relationships, but the anatomical structure. In most, if not all instances, the mitrate calyptra is the result of convergent evolution and does not reflect community of descent. On the basis of anatomical structure, Janzen considered the orthotrichaceous calyptra to be quite different than that of Encalypta.

The cellular structure of the leaves is very uniform in species of Encalypta. The upper laminal cells are more-or-less isodiametric with the walls bulging and papillose on both surfaces, while the basal cells are oblong with the walls more-or-less plane and smooth. Superficially, such features also characterize many species of Orthotrichaceae, Grimmiaceae and Pottiaceae. However, the greatest similarity is between Encalypta and the subfamily Pottioideae of the Pottiaceae, particularly the genera Tortula and Desmatodon. In fact, the resemblances between some species of Encalypta and Tortula are so great, not only in details of the vegetative plants, but also in other characters, as to suggest that they are not merely coincidental.

In superficial view, the upper cell walls are only slightly thickened in species of Tortula and Desmatodon, as they are in Encalypta, and the papillae are generally distinctly "c"-shaped, as in most species of Encalypta. Saito (1975) reported that "The marginal cells are not generally differentiated from the inner laminal cells, but in some species (Barbula hiroshii, Bryoerythrophyllum wallichii), two to three (rarely four) cell-rows are smaller and more thick-walled than the inner laminal cells and are smooth though the laminal cells are papillose.". However, I have observed upper marginal cells more subtly differentiated in some species of Tortula and Desmatodon, exactly as they are in all species of Encalypta. That is, the outer row of cells are slightly differentiated in shape and in the somewhat thickened cell walls. The lumina are ovate with the narrower end oriented perpendicular to the margin of the leaf, so that they appear as a row of eggs placed sideways instead of sitting upright in line with the length of the leaf. The basal laminal cells of species of Tortula and Desmatodon are very comparable in size and shape to those of species of Encalypta, and can be differentiated only by the lack of thickened, transverse walls. The pores that occur in the superficial and transverse walls of the basal cells of some species of Encalypta have not been reported to occur in the

Pottioideae, but are also found in the Calymperaceae (Edwards 1980), which is generally considered to be a highly derived pottiaceous family. A well-known characteristic of the Pottioideae is that in a transverse section of the costa there is only an abaxial stereid band. As a general rule, there are no stereids adaxially. In species of *Encalypta* and in *Bryobrittonia*, there is never any question of an adaxial stereid band, and the papillose upper laminal cells form the adaxial epidermis just as they do in species of *Tortula* and *Desmatodon*. Overall, the similarities between vegetative plants of *Encalypta* and those of some species of *Tortula* and *Desmatodon* are so strong as to make them virtually indistinguishable except with the aid of a compound microscope. This striking similarity has occasionally resulted in taxonomic misinterpretations. For example, Carl Müller (1896) described plants of a *Tortula* species as *E. breviseta* var. *medioseta* and from the same specimen he described plants of *E. ciliata* as *E. breviseta* (see Nomenclatural Notes under *E. ciliata*).

There are several other features of the Pottioideae that suggest a relationship with the Encalyptaceae. The transverse section of the seta of *Desmatodon laureri* (Schultz) B.S.G., figured by Saito (1975), is virtually indistinguishable from that of the Encalyptaceae. The narrowly cylindric, elongate capsules of some species of *Tortula* are vaguely reminiscent of those that characterize *E. streptocarpa* in particular, but also *B. longipes* and *E. procera*. Furthermore, some species of *Tortula* have a well-developed revoluble annulus just like that of *B. longipes*, *E. streptocarpa* and *E. procera*. Saito (1975) reported that chromosome numbers in the Pottiaceae are very variable, but that n=13 is the most prevalent with n=12, 14 and 26 occurring very frequently. Most of the chromosome numbers reported in the Pottiaceae have also been reported in the Encalyptaceae and, as noted in the Introduction, n=13 is the most frequent number and n=26 is next in order of frequency.

The ultimate indication of affinity should be similarities in the structure of the peristome, and in this respect a close relationship between the Encalyptaceae and the Pottioideae may be more difficult to rationalize. The pottioid peristome is unquestionably of the haplolepideoid type, but there are numerous variations in the structure of the teeth in the different genera, from the more-or-less grimmioid shape in *Desmatodon* to the elaborate, twisted peristome of filiform teeth arising from a high, basal membrane in species of Tortula. As is discussed in the Introduction, Philibert (1884) reported that there are both diplolepideous and haplolepideous peristomes in different species of Encalypta, his criteria being that a diplolepideous peristome consists of one or two rows of teeth with a vertical division in the middle of each tooth in the outer row (Figs. 47-49) and that a haplolepideous peristome consists of one layer of teeth with no vertical division on the outer surface of each tooth (Figs. 50-51). On the basis of independent studies of the fundamental structure of the different peristome-types that occur in species of Encalypta, I fully support Philibert's conclusion on the basis of the criteria that he was using. However, with respect to the Pottioideae, the species of Encalypta that bear the strongest resemblance, on the basis of characters other than the peristome, are not the species with a haplolepideoid peristome, E. ciliata and E. rhaptocarpa, but the species with a diplolepideous peristome, E. procera and E. streptocarpa. Furthermore, there are certain general similarities in the form of the peristome of these species of Encalypta and the peristome found in the genus Tortula. The peristome teeth are remarkably long in both the E. procera-E. streptocarpa group (Figs. 83, 98) and in species of Tortula. Also, in these species of Encalypta, the long segments of the endostome are fused basally in a high membrane and it is not too far-fetched to suggest that if the exostome were removed, this endostome could be transformed into a Tortula peristome by a simple twist of the whole apparatus.

There is one basic difference in structure between the pottioid peristome (as well as all haplolepideous peristomes) and the endostome of the E. procera-E. streptocarpa group. Edwards (1979) showed that on the inner surface of all haplolepideous peristomes, there are three vertical divisions for every two peristome teeth, while on the inner surface of the diplolepideous endostome the number is variable, but never three. He also reported that in all species of Encalypta examined, there are four vertical divisions. I have examined the structure of the inner surface of the endostome or peristome of every peristomate species of Encalypta and can confirm Edwards' report (Figs. 57, 60, 62). If the above evidence, which suggests that the Encalyptaceae are most closely related to the Pottiaceae is accepted, then this fundamental difference in structure may have great significance, for it appears to support Philibert's original suggestion that the Encalyptaceae are a basal group from which the haplolepideae and diplolepideae are derived. However, I would modify this basic idea. The Encalyptaceae are probably a relatively advanced group that have retained some plesiomorphous character-states, particularly in the structure of the peristome. But they probably share a common ancestor with the Pottioideae and have retained more of the features of the diplolepideous stock. A pseudohaplolepideous peristome has arisen within the Encalyptaceae in E. rhaptocarpa and E. ciliata, but the links with haplolepideous mosses are not through these species, but through the species of Encalyptaceae with the most plesiomorphous character-states, E. streptocarpa, E. procera and B. longipes. Similarly, the connections with diplolepideous mosses are to be sought in this group of the Encalyptaceae and in this regard the position of the exostome teeth opposite the endostome segments (Fig. 47) is of significance (Vitt 1981).

There are very few mosses with diplolepideous peristomes that have the exostome teeth opposite the endostome segments. In the majority of instances, they are alternate. The peristome teeth are opposite in the Funariaceae, Buxbaumiaceae, Splachnaceae and one genus of the Orthotrichaceae. If the Encalyptaceae are considered to be close to the ancestral stock that gave rise to the haplolepideae, then it may well be distantly related to some or all of these groups of mosses. Vitt (1981) has recently suggested that the ancestral type among the Bryidae must be close to the Funariaceae with the plesiomorphous character-states of smooth leaf cells and an opposite, deplolepideous peristome. One of the defining features of the genus Bryobrittonia is the smooth leaf cells. In this respect, Bryobrittonia more closely approaches the ancestral type, as hypothesized by Vitt, than a species of Encalypta. However, I suspect that the gametophytic features that differentiate Bryobrittonia from species of Encalypta actually represent derived conditions within the Encalyptaceae. Papillose leaf cells characterize both the species of Encalypta with the most plesiomorphous character-states, E. streptocarpa and E. procera, and the species of Pottioideae with which they appear most closely related. If the Encalyptaceae and the Pottioideae are derived from a common ancestor, the most parsimonious explanation is that the ancestral condition, within the Encalyptaceae, was papillose leaf cells. Therefore, Bryobrittonia is considered highly derived in character-states of the gametophyte, but plesiomorphous conditions of the sporophyte have been retained. In the genus Encalypta the direction of evolution seems to have been just the opposite. Evolutionary divergence has been concentrated in characters of the sporophyte. Such a point-of-view does not negate Vitt's hypothesis. It merely implies that the Encalyptaceae are farther removed from the ancestral type in their gametophytic structure than in character-states of the sporophyte.

Evolution of the Encalyptaceae

The centre of distribution of the Encalyptaceae is clearly in the Northern Hemisphere with the greatest concentration of species in northwestern North America, and Scandinavia and the Alps of central Europe. Four of these "Northern Hemisphere" species of Encalypta, E. ciliata, E. procera, E. rhaptocarpa and E. vulgaris, occur sporadically in widely disjunct localities in the Southern Hemisphere. As well, there are two species, E. armata and E. asperifolia, that are narrowly endemic to the Andes of South America. Most species of Encalyptaceae in the Northern Hemisphere occur on both the North American and the Eurasian continents. However, two species are endemic to North America, E. flowersiana and E. vittiana, and E. streptocarpa probably does not occur in North America. Encalypta microstoma is endemic to Europe. Bryobrittonia longipes and most species of Encalypta are restricted to montane and secondarily to arctic regions, but a few are more widespread and are also found across the boreal zone. These include E. ciliata and E. rhaptocarpa, and E. procera (in North America, but in Eurasia it is restricted to Scandinavia and central Asia) and E. streptocarpa (in Europe).

The very fact that there are marked differences in the distribution patterns of different species of Encalyptaceae, as outlined above, indicates that these patterns are not the result of random dispersal. Their character reflects vicissitudes of the earth's environment and history. Species of Encalyptaceae are presently concentrated in the Northern Hemisphere, but this cannot necessarily be taken as an indication that they evolved there (Schuster 1976). The ancestral type could have evolved in the Southern Hemisphere, migrated into the Northern Hemisphere and radiated there. However, three of the four Northern Hemisphere species, E. ciliata, E. rhaptocarpa and E. vulgaris, that occur in the Southern Hemisphere are considered to be rather highly derived members of the Encalyptaceae, as are the two species endemic to South America. Furthermore, of the two species of Encalyptaceae with the most plesiomorphous character-states, B. longipes occurs only in very northerly regions of the Northern Hemisphere, and E. streptocarpa is restricted to Eurasia. Therefore, it seems most plausible to suggest that the Encalyptaceae evolved in the Northern Hemisphere. As Bryobrittonia and many of the species of Encalypta are found both in North America and Eurasia, it also seems most likely that the family evolved after the separation of Laurasia and Gondwanaland in late Jurassic times, but before the division of Laurasia in the upper Cretaceous. It also seems that many species of Encalypta, even including some that are considered to be quite highly derived, had evolved prior to the separation of the northern continents, or perhaps around the time of separation. For example, E. brevipes is characterized by highly apomorphous character-states of a short calyptra, very short seta and gymnostomous capsule. Yet the distribution pattern appears to be old. Encalypta brevipes is known from a very few localities; however, these are scattered around the Northern Hemisphere (Fig. 188) and the populations are almost always very sparse. Another example is E. spathulata. It is also highly derived in many structural features, similar to E. brevipes. It is known from a number of quite widely scattered localities in Europe, but in North America it is very narrowly restricted (Figs. 260, 261). The distribution patterns of both of these species must be relictual and they indicate that not all of the species with many apomorphous character-states are recently evolved. However, several appear to be. Encalypta armata, E. asperifolia, E. microstoma and E. flowersiana are all narrow endemics, and all are characterized by many highly derived features. For example, the spines on the leaves and calyptra of E. armata, the lack of a peristome in all four species, the vermiform protuberances on the spores of E. flowersiana and so forth. These species must all have evolved relatively recently. Encaypta microstoma and E. flowersiana have presumably evolved during the Tertiary since the division of Laurasia, and E. armata and E. asperifolia most likely are derivatives of E. vulgaris that have evolved since the Andean orogeny in late Tertiary times.

It is a conspicuous feature that in the case of the rarest species of Encalypta, there are almost invariably more collections and the populations are generally more extensive in western North America than in Eurasia. This probably reflects the combined effects of anthropogenic influences and glaciation. During the Wisconsinan glaciations in

Europe, many plants are known to have survived south of the glacial boundary in the Alps and it has been suggested that some survived in refugial areas in Scandinavia within the glacial boundaries. However, the populations that did survive there have been subject to the influence of man's activities for a much longer time than in western North America. The rarer species of Encalyptaceae in western North America are almost all distributed north of the glacial boundary and it seems likely that most of them survived glaciation in the unglaciated areas of Beringia or farther south in montane refugia. Because there were such extensive areas in Beringia that were not glaciated and the advent of 'civilized' man in western North America has been a relatively recent event, it appears that the arctic–montane flora that has survived is a rich one by comparison to Europe.

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